VOLUME LXV NUMBER 6

THE
BOTANICAL GAZETTE

JUNE 1918

SUCCESSIONS OF VEGETATION IN BOULDER PARK, COLORADO

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 238

W. W. ROBBINS

(WITH FOURTEEN FIGURES)

Introduction

This paper is concerned chiefly with the plant successions of the flood plains, lakes, and ponds of a mountain park. They culminate in a temporary meadow climax. Consideration is also given to the succession which begins on the xerophytic glacial gravels and passes through the characteristic and long persistent "dry grassland" stage also to a temporary meadow climax. There is also presented the interesting problem of the genetic relation of the meadow to the forests of aspen, lodgepole pine, and Engelmann spruce-balsam fir which border the open park. It should be stated that Boulder Park is typical, in its physiographic and vegetative development, of hundreds of such areas in the Rocky Mountain region.

Boulder Park is located in Gilpin County, Colorado, about 34 miles, in a straight line, west of Denver. The Divide of the main range of the Rocky Mountains is about 6 miles west; the Great Plains are about 18 miles east. Tolland, a small town near the middle of the Park, has an altitude of 8889 feet. The area falls within the montane zone (10).

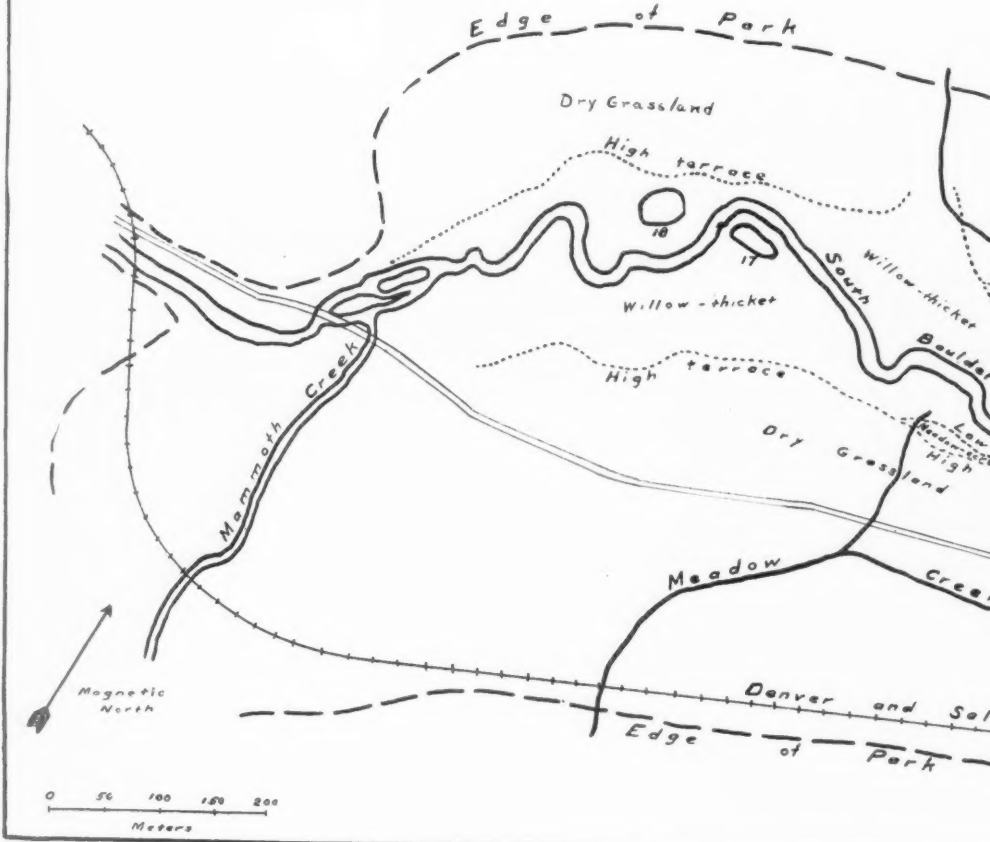
Boulder Park was selected as the site for the University of Colorado Mountain Laboratory, the first session being held in the summer of 1909. Several papers (**11, 12, 19**) have been issued setting forth the facilities for field study at the Laboratory, but also presenting certain botanical features of the neighboring vegetation. Other papers dealing exclusively with the plant life of the Park and adjacent territory are referred to in this paper.

Topography and physiographic history

GENERAL.—The term "park" as used throughout the Rocky Mountain region refers to an open, flat, usually grassy area in the mountains. Such areas may be large, including 100 or more square miles; or small, containing only a portion of a square mile, and often possess a scattered growth of trees. Boulder Park is the broadened valley of South Boulder Creek. It is generally level, and through it flows the stream which is slowly working its way back and forth and producing well defined flood plains. The level portion of the park proper is bordered by steep slopes, the crests of which are 500–1000 ft. above the valley floor. The slopes have been burned over in large part, and exhibit various stages of the "burn succession," the most obvious of which are lodgepole pine and aspen. The climatic climax forest of Engelmann spruce-balsam fir is found in places. Some typical talus slopes occur. The country granitic rock is exposed in rugged outline in places, and may be observed in different stages of disintegration and decomposition, and in various stages of vegetative development. The building of the Moffat Railroad has created deep rock and gravel cuts, gravel and rock heaps and slides, often resembling talus and natural slides; likewise, the building of wagon roads has made many new areas whereupon secondary succession may be observed. The general topographic features of the Park may be seen by referring to figs. 1–3.

In Pleistocene times this area and many others in the mountains of Colorado were glaciated. The glaciers had their heads above timber line and moved down the valleys, leaving evidence of their action. The ice which was largely instrumental in shaping and modifying the topography of Boulder Park came from two sources,

BOULDER PARK



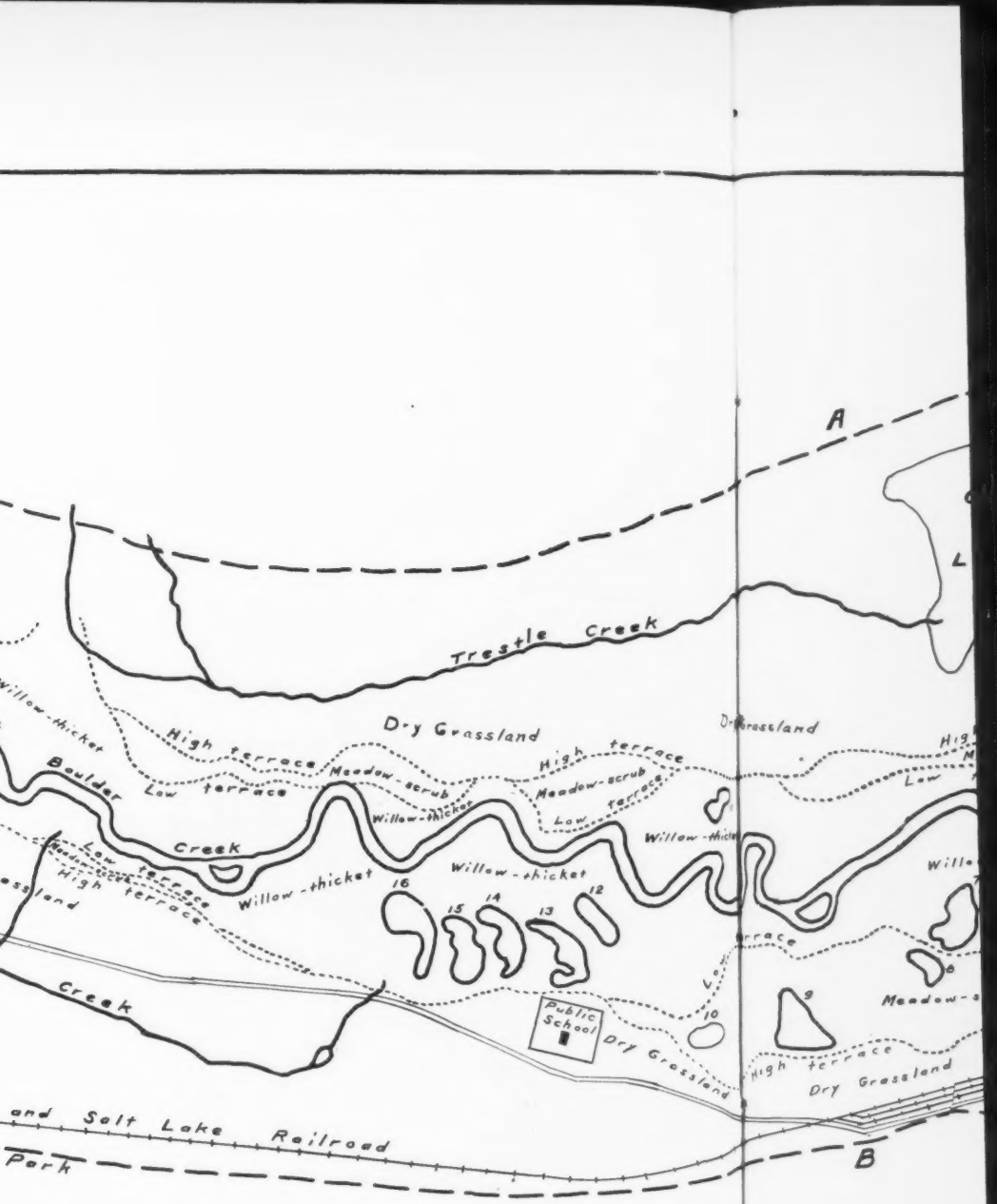
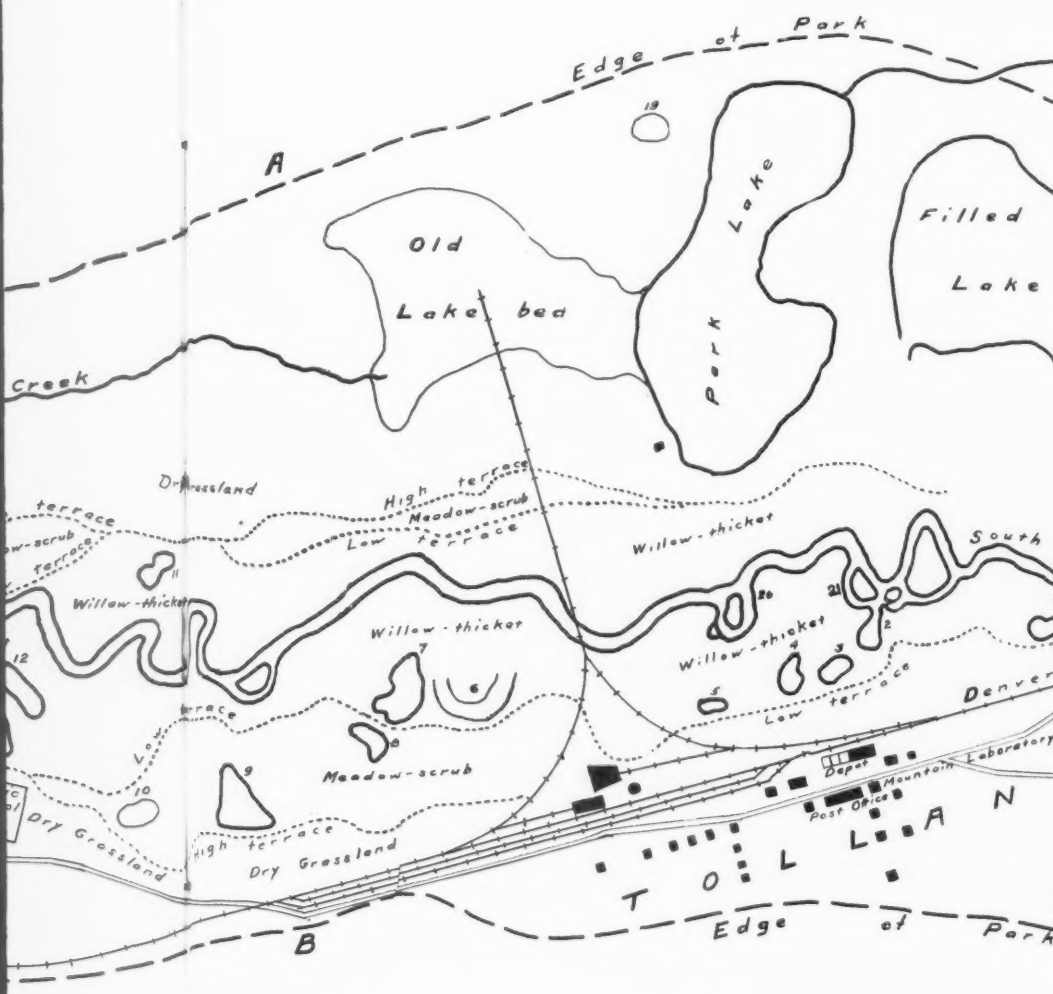
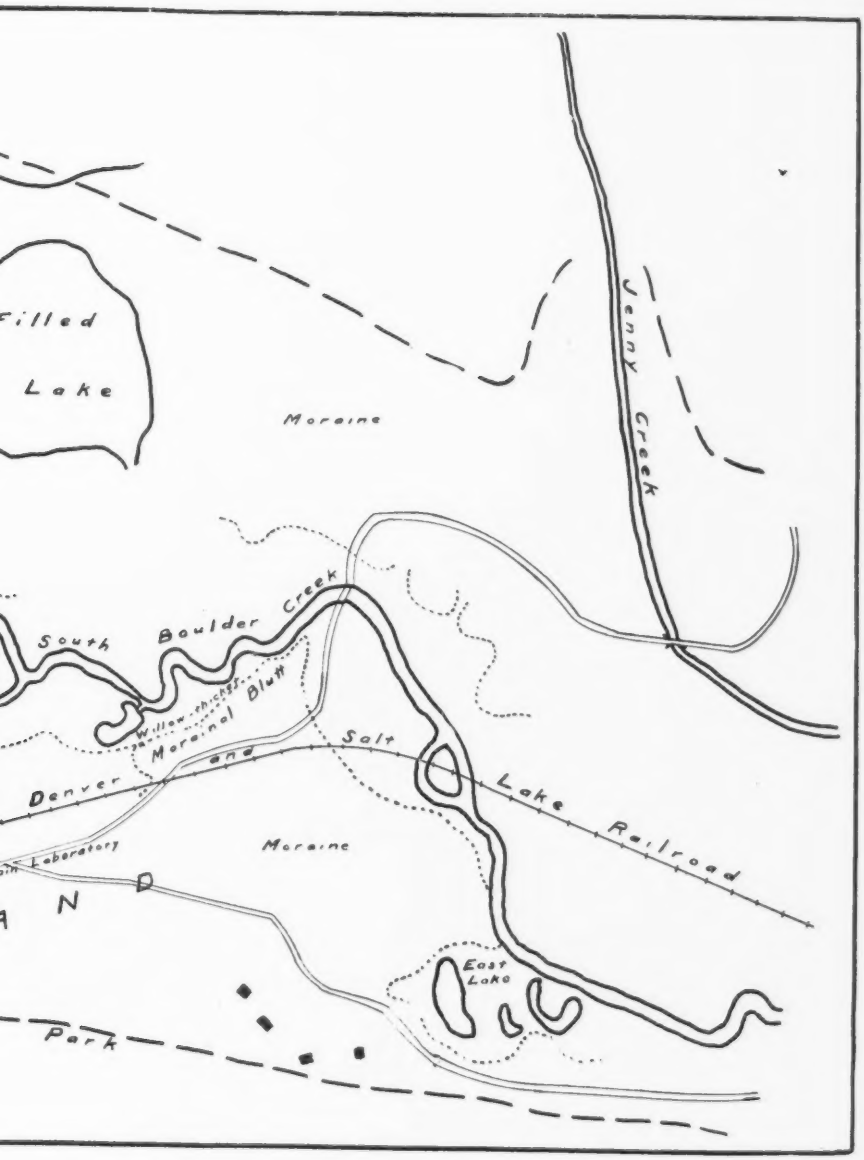


FIG. 1.—Map of Boulder Park (surveyed by G. S. DODDS, W. L. BROSIUS, and W.



ark (surveyed by G. S. Dodds, W. L. Brosius, and W. W. Robbins)


Filled
Lake
Moraine
Jenny Creek
South Boulder Creek
Willow-thicket
Moraine
Moraine
Denver and Salt Lake Railroad
Laboratory
Moraine
East Lake
Park

South Boulder Canyon and Mammoth Gulch. The two bodies of ice no doubt met at the upper end of the Park and filled it to a depth of 400–550 ft., as is evidenced by the elevation of perched boulders on both slopes bordering the Park. Below Tolland is an area of hummocky topography typically morainal. The hummocks and the depressions between are strewn with rounded boulders, so much weathered that all traces of glacial scratches are obliterated. Post-glacial stream action has washed away great quantities of this terminal moraine. Lateral moraines join with the terminal and extend up the valley on the sides of the ridges. There is also a very wide and deep morainal deposit at the mouth of Mammoth Gulch. A comparatively small amount of it has been carried away. At the entrance of South Boulder Canyon, however,

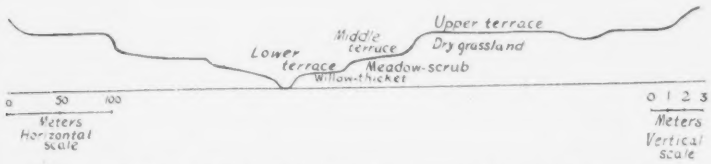


FIG. 2.—Profile of Boulder Park along line extending from *A* to *B* in fig. 1

but small remnants of moraine remain. This is undoubtedly due to the fact that South Boulder is a much larger stream than Mammoth, and since the retreat of the glacier it has carried away almost all of its moraine.

It has just been indicated that there are two large distinct deposits of morainal material in the Park: one below Tolland, the other at the mouth of Mammoth Gulch. They probably represent the terminals of two distinct glacial bodies of ice belonging to different periods of glaciation. In all instances where investigations (**1, 4, 7, 8, 9, 23, 26**) of the epochs of glaciation have been made in the western mountains, there have been two distinct epochs, and furthermore, in each case the earlier glacier extended farther than the later.

ORIGIN OF TERRACES.—The foregoing has been given in order to make clear the origin of the ponds and terraces which are such prominent features of the Park's topography. Figs. 1 and 2 show

that there are 3 main levels bordering the stream: (1) Low terraces, into which the present stream is now cutting. During high waters a portion of this may be inundated. Gravel is overlaid with a deposit of peat, ranging in depth from an inch or so to 3 or 4 ft. This level is covered with a willow thicket association in which the dominant forms are *Salix chlorophylla* Anders. and

FIG. 3.—View of Boulder Park looking west: James Peak at left and Continental Divide in background; glimpses of stream may be seen flowing through willow thicket association; note lighter colored patches of dry grassland; slopes are clothed with aspen, lodgepole pine, and Engelmann spruce-subalpine fir.

S. padophylla Rydb. (2) Middle terraces, meander terraces much older than the preceding. On the middle level the gravel is not overlaid with peat, except in a few places. The soil is a sandy and gravelly loam and 4–8 inches deep. The characteristic vegetation is meadow scrub in which *Salix glaucops* Anders., *Betula glandulosa* Sarg., *Dasiophora fruticosa* (L.) Rydb., and mesophytic herbs are dominant. (3) High terraces, which are composed of glacial gravels which have been worked over by the stream which issued from the

end of the retreating glacier. Typically, there is little accumulation of humus upon them. The vegetation is a "dry grassland."

The terminal moraine below Tolland undoubtedly acted as a dam to the stream coming from the glacial front, and for a long time the Park was the site of a lake. Subsequent to the period of deposition, the stream was lightened of its load and immediately began to cut into the terminal dam, which being of easily eroded material was quickly cut through. This resulted in a rapid drainage of the lake and the formation of a high terrace on each side of the stream issuing from the glacial front. The middle terraces are of stream origin.

ORIGIN OF LAKES AND PONDS.—With the exception of Park and Filled Lakes, all the natural ponds in the Park are of oxbow origin. Park and Filled Lakes are the largest and deepest. Their depth alone shows that they are not of oxbow origin. In the center of Filled Lake the peat is over 10 ft. deep. At no other point in the Park is there such a deep peat deposit. The relation these two lakes bear to the higher level shows that they were not formed during the deposition of the material composing this level. On the retreat of the first glacier two large ice cores were left on the valley floor. Hence, when the wash from the later terminal was brought down the valley it was deposited about the edges of these débris covered bodies of ice. The ice melted later, leaving the two lakes, Park and Filled.

Climatic factors

There are no extended climatic records for Boulder Park. ROBBINS (**22**) has shown the following average temperature and precipitation relations to exist in the "lodgepole pine forest zone" of Colorado, and from these a notion may be gained of climatic conditions in Boulder Park.

Mean annual temperature	34.9° F.
Mean winter temperature	18.4°
Mean spring temperature	33.4°
Mean summer temperature	53.6°
Mean fall temperature	38.4°
Average length of frostless season	67 days
Average date of last spring frost	June 20
Average date of first fall frost	September 9
Absolute annual range of temperature	104 days
Mean annual precipitation	25.53 inches
Mean annual snowfall	112.9 inches

During a portion of the growing seasons of 1909 and 1913, thermographs were run by members of the staff of the Mountain Laboratory. They show that the daily range of temperature may run high. This is particularly the case during clear weather. The daily minimum temperature is usually reached between 5:00 and 6:00 A.M., the daily maximum between 1:00 and 2:00 P.M. In 1909 the latest freezing temperature was June 22; in 1913 the temperature sometimes went down to freezing or below throughout July, and on August 1 of that year the minimum was 32° F. Afternoon showers of short duration during June, July, and August are common. Prolonged rains are infrequent. Although there is considerable snow, its accumulation on the high terraces, particularly, is largely prevented by their exposure to the sweep of winds from the west. There are large drifts of snow, however, in protected situations.

RAMALEY and MITCHELL (**18**) in 1909 determined the relative humidity at a number of Park stations. It varied on July 8 from 39 per cent on the north exposure of a railroad cut to 65 per cent in the lodgepole pine forest; on July 12, from 39 per cent in the railroad cut to 71 per cent in the forest.

Successions

FLOOD PLAIN SUCCESSION

Boulder Creek is a meandering stream with considerable cutting power. Along its course in the Park one may find shores of erosion, of deposition, and numerous oxbows in all physiographic and vegetative stages, and also well defined stream terraces. Hence there is an unexcelled opportunity here, as may be judged somewhat from a reference to fig. 1, to study succession on a mountain flood plain.

Two types of embryonic flood plains occur along Boulder Creek in its course through the Park: (1) those composed of well rounded boulders (cobblestones), averaging 2–6 inches in diameter, with a slight admixture of coarse gravel (fig. 4); and (2) those made of sand and silt (fig. 5). The former are initially xerophytic, the latter hydrophytic.

Shores of the cobblestone type may be partly under water during the spring or in wet seasons, but are usually bare in summer and

during dry years. The temperature extremes are great. Furthermore, the occurrence of flood-waters postpones the invasion of pioneers. The freshly exposed stones and gravel possess no vegetation. Algae which may have been clinging to rocks while submerged are killed on exposure to the sun. There is no lichen stage on the rock surfaces. The first plants gain a foothold in

FIG. 4.—Along South Boulder Creek: flood plain of cobblestones invaded by highly mixed plant community; note zone of *Carex variabilis* bordered outwardly by willow thicket.

the meager accumulation of fine sediment between the stones. *Agrostis hiemalis* (Walt.) B.S.P. and moss species usually initiate the succession. The individual grass plants form an interlacing, dense mass of fibrous roots which collect and hold sand and silt. These initial plants are followed by a highly mixed community composed of migrants from the sedge moor, willow thicket, meadow, and even dry grassland; in fact, there is no new habitat in the Park, except it is the roadside, where there is such a great number

of different species. The principal invaders are *Deschampsia caespitosa* (L.) Beauv., *Phleum alpinum* L., *Poa alpina* L., *Sporobolus brevifolius* (Nutt.) Scribn., *Carex variabilis* Bailey, *Salix chlorophylla* Anders., *S. padophylla* Rydb., *Sedum rhodanthum* Gray, and *Dodecatheon radicatum* Greene. The occurrence here of a depauperate form of *Erigeron eximius* Greene is interesting, as

FIG. 5.—Invasion of flood plain of sand and silt: note openness of vegetation, advancing clumps of *Agrostis hiemalis* and *Alopecurus fulvus*, and society of young *Salix chlorophylla* and *S. padophylla* shrubs.

is also the presence of such species as *Festuca ingrata* (Hack.) Rydb., *Rumex acetosella* L., *Arenaria Fendleri* Gray, *Sedum stenopetalum* Pursh, and *Dasiophora fruticosa*. In spite of the large number of species, the community is open. As vegetative development proceeds there is a reduction in the number of species and an increase in the number of individuals of the successful species, and increasing mesophytism of the habitat.

As is quite commonly the rule on flood plains, the first woody plants to gain a footing are *Salix* species. In this case the invaders are *S. chlorophylla* and *S. padophylla* (figs. 4, 5). After a few years a willow thicket is formed; at the present time extensive willow thickets prevail along the whole course of the stream on ground not far removed from the water level. The willow thicket has a peat deposit from a few inches to over 3 ft. deep. As has been indicated, the water level is near the surface at all times, and the association may undergo flooding in the early season.

In the series of successions starting with gravelly and stony stream banks, willow thicket is replaced by a meadow scrub. The presence of tall willows about a terrace lake in the Park has come to be looked upon as evidence of its oxbow origin. The dying out of tall willows in the drier portions of the willow thicket, the quite common presence of relicts of willow thicket throughout the meadow scrub, and the occurrence of small patches of meadow scrub throughout the willow thicket, are all evidences that willow thicket is being succeeded by meadow scrub. Such relicts are usually represented by a few tall *Salix padophylla* and *S. chlorophylla* shrubs, and in almost all instances such individuals possess many dead branches.

Meadow scrub attains its typical structure on the middle stream terrace. The characteristic shrubs are *Salix glaucops* and *Dasiophora fruticosa*, both of which are low forms as compared with those shrubs dominating the willow thicket. The herbs are those found in the herbaceous meadow of the Park. Meadow scrub commonly has a striking hummocky character. This is due to herbs building up about the shrubs. In places *Dasiophora* dominates the association. This shrub stands about 18 inches high, and the individuals usually 2 or 3 ft. apart. It has a considerable habitat range. In the progressive drying of the meadow scrub, it lags behind as a relict. It is, on the other hand, a common invader of the sedge moor.

The fact that meadow scrub on the middle terrace is laid on gravel indicates that the stream must have moved laterally rapidly on that level, thus giving little opportunity for the development of peat. At the present time the stream is swinging back and forth

across the valley at a comparatively slow rate, as is witnessed by the formation of peat on the recent levels.

Occasionally sedge moor may precede willow thicket on stream banks, and it is not at all uncommon to find stream banks of shingle remain xerophytic for a long period. The small isolated dry grassland patches throughout the willow thicket association are undoubtedly of this type.

Where the meander approaches its maximum curvature, the force of the stream on the inside of the curve is so slight that fine material is freely deposited. A good illustration of this is to be seen in oxbow 20 (fig. 5). The main current flows through the cut-off channel. A small portion of the stream with only slight carrying power still flows through the oxbow. It has built up a sandy and muddy stream flat. Such a habitat as this has a varied vegetative history. Usually, an association of *Eleocharis-Ranunculus* is the first to become established. This is the characteristic amphibious community of the Park. The principal species are *Eleocharis acicularis* (L.) R. and S., *E. palustris* (L.) R. and S., *Ranunculus reptans* L., *R. natans* L., *Allocarya scopulorum* Greene, and *Alopecurus fulvus* (L.) R. and S. *Eleocharis acicularis* builds a dense turf or mat. *Allocarya scopulorum* may also grow so thickly as to form a rather close growth over the soil surface. *Alopecurus fulvus* is a constant principal species of the community. *Eleocharis acicularis* often grows into several inches of water; such plants are sterile. However, by a slight lowering of the water level, the plants spread rapidly both by the underground parts and by seed, and in one season may make good headway toward reclamation of the mud flat exposed. *Eleocharis palustris* (fig. 6) finds its best expression in some of the oxbow lakes, especially those that have a flat, stony, or gravelly bottom and possess water only a part of the year. In oxbow lakes 8 and 9, for example, almost the entire area over which water stands, for a time at least, is covered with *Eleocharis palustris* and *Ranunculus reptans*. Rare associates are *Glyceria borealis* (Nash) A. Nels. and *G. grandis* Wats.

The *Eleocharis-Ranunculus* association is followed usually by sedge moor, in which *Carex variabilis* is the predominant species,

and this by a willow thicket of *Salix chlorophylla* and *S. padophylla*, or in certain instances the mud flat along streams may be invaded directly by *Salix* species, and still in other cases, especially where the soil is sandy rather than muddy, *Agrostis* is initial and is followed by a mixed community similar to that on more gravelly

FIG. 6.—Along shore of oxbow lake 9: at shore edge there is an almost pure association of *Carex utriculata;* bordered on water side by *Eleocharis palustris-Ranunculus* association; tall willows on farther side are relicts of willow thicket stage.

stream banks. This is replaced by willow thicket, which in turn gives way to a mesophytic grassland or meadow scrub.

Oxbow 20 (fig. 7) represents an oxbow in an early stage of formation. Some water is still flowing through the old channel (*egh*). The cut-off is clearly marked. From *c* to *d* a sand bar is being constructed and now almost reaches the water surface and extends from shore to shore. The outlet end of the oxbow will, of course, be the first to close. Then will follow the filling of the inlet, thus completing the formation of a closed body of water having the

shape of a bow. The shores of the newly formed lake have steep, vertical sides on the outside of the stream curve. On the inside

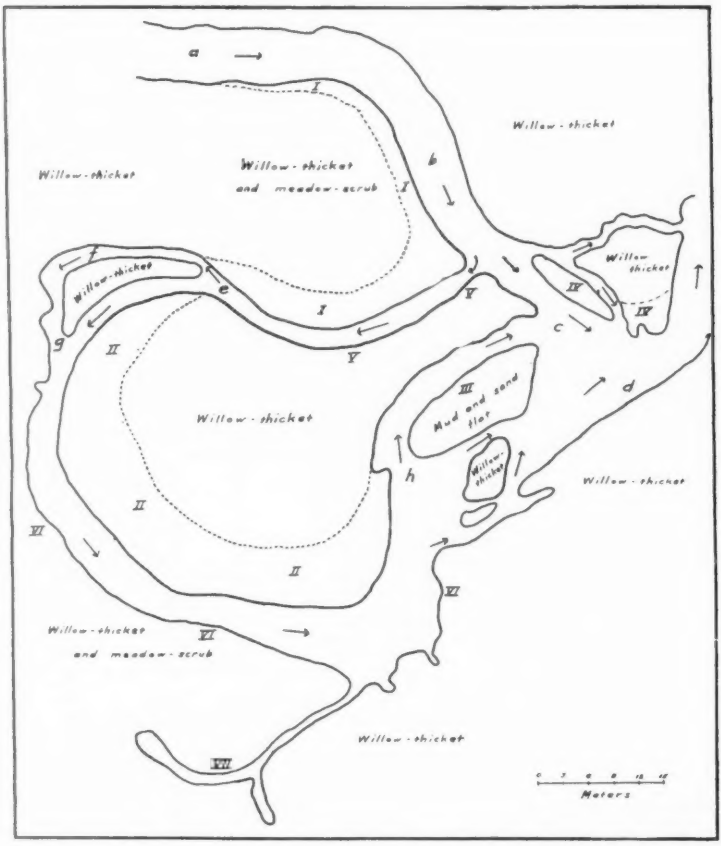


FIG. 7.—Map of oxbow no. 20: an early stage in the development of an oxbow lake; main stream occupies channel *abcd;* some water still flows through old channel (*cgh*); from *c* to *d* a sand bar is being deposited; shore no. I, composed of sand, gravel, and boulders; at high water the strip may be covered; shore no. II, composed of gravel, sand, and fine silt; the bare soil is being invaded by a mixed association; shore no. III, a mud and sand flat under water a good part of the year; shore no. IV, cobblestone on which no vegetation has secured foothold; shores nos. V and VI, perpendicular erosion shores; "runs" of the kind shown at no. VII are common throughout the Park, being very narrow and with vertical walls.

of the curves there are gravelly, sandy, or muddy shores of deposition. The future history of this lake is now largely concerned with the activities of plants. In the developing of this oxbow lake *Callitriche palustris* L. and *Batrachium trichophyllum* (Chaix.) Bossch. are the first representatives of pond life. The main stream throughout the Park is too swift to allow the growth of any vegetation within it except algae, chiefly *Draparnaldia acuta* (Agardh) Kuetz. and *Prasiola mexicana* J. G. Agardh. These are attached to the rocks in the stream bed. They flourish only in swift running water. *Batrachium trichophyllum* and *Callitriche* have appeared in the still water back of the sand bar. Encroachment by the vegetation now starts in from all sides, and the area quickly comes to willow thicket. *Carex utriculata* sometimes becomes interpolated at the margin between willow thicket and open water. It is an important invader of these shallow oxbows. It is frequently succeeded by *Carex variabilis*, which is in turn followed by willow thicket. An oxbow that has had its connection with the main current severed usually passes through the same stages of succession found about lake shores.

Oxbow 3 is a somewhat different type from the preceding. The lake is shallow and has a muddy bottom, over which numerous small rocks are scattered. The orignal rock and gravel stream bed is thus still visible. The lake is free from water during the latter part of the season. *Alopecurus fulvus* is dominant on the muddy bottom. Associates are *Ranunculus reptans*, *Eleocharis acicularis*, and *Sparganium angustifolium* Michx. *Carex utriculata* is rapidly invading the *Alopecurus* society. Mixed with *Carex* is *Glyceria americana*, *Alopecurus fulvus*, and a great deal of moss. Moss often invades the *Carex utriculata* association, preparing a substratum upon which willow thicket may build more readily.

Oxbow 5 is a small and shallow pond which undergoes periodic drying. There is a well developed *Eleocharis-Ranunculus* association on the sandy bottom. It is being invaded by *Carex utriculata*, after which comes willow thicket.

Oxbow 6 exhibits a pond that is now almost filled with vegetation. A very small area of open water still remains. The lake was narrow and filled in a manner normal to gravelly or muddy shores,

that is, by the invasion of willow thicket. There is no vestige, however, of the first associations of these shores. *Carex utriculata* occupies the wettest part of the area. It is followed on all sides by the springy sedge moor of *Hypnum*, *Carex variabilis*, and *C. canescens* L. Here *Carex variabilis* is building upon the moss. The principal shrub succeeding *C. variabilis* is *Salix chlorophylla*.

Oxbow lakes 8 and 9 differ in a marked degree from all others in the Park. It will be seen that they are the only lakes of oxbow origin that occur on the middle terrace. Obviously they are physiographically much older than those of the lower stream terrace. They are very shallow and annually dry up. In spite of their age, they have not filled to any extent. Rock and coarse gravel, with but comparatively little finer material between, make up the pond bottom. This lack of plant débris is associated with periodic drying, and the exposure of the area to the winds. Late in a particularly dry season, the level bottom becomes dry and the strong winds blow away the material that accumulates. The chief associations over almost the entire lake bottom is an open one of *Eleocharis palustris* and *Ranunculus reptans* (fig. 6). *Glyceria borealis* and *G. grandis* are rare associates. About the shore edge *Carex utriculata* is slowly working inward. *Carex variabilis* or meadow scrub may come to the water's edge. A few clumps of *Salix chlorophylla* and *S. padophylla* at the edge are relicts of the old stream bank stage. Such individuals have numerous dead and dying branches.

East Lake (figs. 8, 9) is an old oxbow of South Boulder Creek, from which it is now separated by about 250 ft. The intervening area is a sedge moor alternating with willow thicket. Through this the lake outlet feebly flows. The old shore line of the creek is distinct. *Mertensia ciliata* (Torr.) Don. and *Senecio triangularis* Hook., typical streamside plants in the region, may be found sparingly in the willow thicket of the lake. *Salix chlorophylla* and *S. padophylla*, with the two associated herbaceous species, are relicts of a streamside flora. There is further evidence of the oxbow origin of East Lake. The stream cut into the terminal moraine and made a strong curve toward the southwest, working into its bank almost at right angles. As is happening at many places in the present

stream course, the shores were eroded and an inlet of considerable width and depth formed. We take it that the position of this is represented by the long tongue of sedge moor that extends from the lake edge to the meadow. Soil borings here show deep deposits of peat extending to the meadow.

At present, East Lake has a flat bottom and a uniform depth of about 1 ft. The bottom is of mud. The lake's development is

FIG. 8.—View of East Lake, of oxbow origin; beyond is portion of large terminal moraine.

natural and typical of an oxbow belonging to the lower terrace. The associations in and about the pond are arranged concentrically, particularly along the west and south sides. A small amount of *Batrachium* and *Callitriche* is found in the water. *Carex utriculata* makes a pure association chiefly along the west shore, where it is rapidly pushing out into the water. The plant is 1–2 ft. high and spreads by means of creeping rootstocks. Its typical habitat is still water not exceeding 1 ft. in depth. The amount of plant remains annually deposited by it is considerable. Furthermore, it

breaks wave action and thereby facilitates the accumulation of sediment between its closely crowded erect stalks. It is followed by the typical sedge moor, and this by willow thicket or meadow.

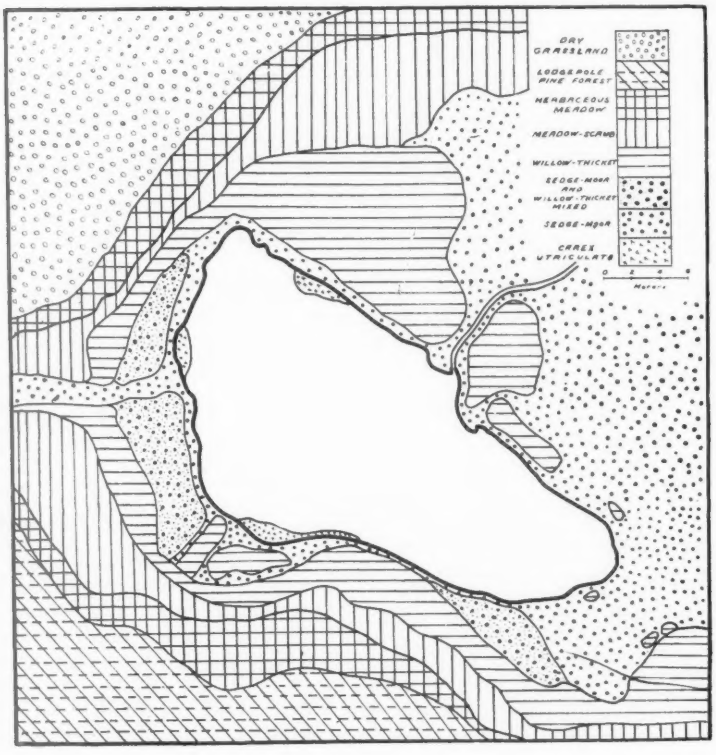


FIG. 9.—Map of East Lake, showing surrounding plant associations

Carex utriculata, however, is not the only agent in the invasion of the open water. Fig. 10 shows a section of the shore edge and sedge moor. It will be noted that there is a distinct elevated rim at the water's edge. This elevated rim is present almost entirely about the lake. Such a rim is commonly found along the streams, and is the result of stream cutting. Its occurrence about a lake may be taken as an evidence of its oxbow origin; not conclusively,

however, for the rim is also a feature of glacial lakes such as Redrock (**20**) and Park, which are not genetically related to stream topography. In these it is no doubt formed by the sapping action of ice. Of course, stream action and ice action may be cooperative factors. At any rate, whatever its origin, once established the rim is maintained by vegetative building. At East Lake the rim about the edge has a mean height of about 16 inches. In texture it is a loose and spongy mass and consists of living and decayed

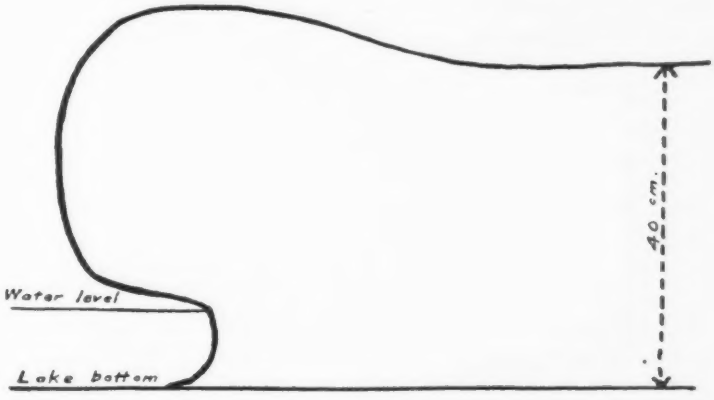


FIG. 10.—Section of "rim" and sedge moor at East Lake: rim which overhangs water has loose and spongy texture and consists of living and decayed plant material, largely masses.

plant material, largely mosses. Just back of the rim the soil is wetter, more compact, and the character of the vegetation somewhat different. Being actually drier than the moor a foot or so landward, it supports an assemblage of plants, many of which would scarcely be expected to grow at the water's edge. *Salix chlorophylla* and *Dasiophora fruticosa* are the important shrubs of the rim. The seeds lodge and germinate on the bare, more or less perpendicular, wall of the rim, and the young plants curve outward and upward over the water. Other characteristic rim plants are *Betula glandulosa*, *Sedum rhodanthum*, *Dodecatheon radicatum*, and *Poa leptocoma* Bong. The importance of moss in the building of the rim should be noted. As the rim slowly builds out over the

water, it sinks by its own weight, thus forming the flatter, lower, and more compact part just back from the edge. Willow thicket is invading the moor in many places. It is replaced by meadow scrub. At several points sedge moor passes directly into sedge moor, thus omitting the thicket and scrub stages of succession.

The principal species in the sedge moor of Boulder Park is *Carex variabilis*. It is a peat forming species. In reaction, the soil of the sedge moor is very slightly acid. The plants of the association stand close together. There is always an abundance of moss, which is of great importance in the building of peat. The sedge moor becomes marshy during the spring and early summer and after heavy rains. Then, the water aids in the packing down of dead sedge plants. The water table is always high and the soil water content high throughout the year. Stratification occurs to some extent. The following species form a ground layer: *Androsace subumbellata* (A. Nels.) Small, *Galium trifidum* L., *Crunocallis chamissonis* (Esch.) Greene, *Veronica serpyllifolia* L., *Alsine longifolia* (Muhl.) Brit., moss, and liverworts. *Caltha rotundifolia* (Huth.) Greene is an important component of the sedge moor. It is not a shade plant and hence does not do as well in the denser parts of the association as in more open spots.

Petasites sagittata Gray is prevernal in the sedge moor. *Caltha* is the characteristic species of the spring aspect (May 15–July 1). The summer aspect (July 1–August 15) is marked by a large number of sedges, grasses, and other herbs, most important of which are *Carex variabilis*, *Deschampsia caespitosa* (L.) Beauv., *Hierochloa odorata* (L.) R. and S., *Sedum rhodanthum* Gray, *Pedicularis groenlandica* Retz., and *Agrostis hiemalis* (Walt.) B.S.P. The appearance of gentians the latter part of August ushers in the autumn aspect (August 15–October 1). Chief of these are *Pleurogyne fontana* A. Nels. and *Gentiana plebeya* Cham. During the winter the sedge moor is a level expanse of withered shoots and leaves, chiefly *Carex*.

As compared with drier associations, the seasonal aspects of the sedge moor change slowly. The reason for this is partly the fact that *Carex* hides other forms growing within it, and furthermore to the actual paucity of species in this area as compared with drier

situations. More important, however, are soil, temperature, and moisture conditions. The maximum seasonal variations of soil temperature in typical associations during the summer of 1909 (13), as seen in the following table, will give some explanation of the rapidity of change in the seasonal aspects.

Sedge moor	7° F.
Willow thicket	8°
Meadow scrub	16°
Herbaceous meadow	20°
Dry grassland	24°

It will be noted from this that the sedge moor has the least variable soil temperature throughout the growing season. This condition is due for the most part to the amount and texture of the vegetative cover, and also is intimately related to the soil water content. Sedge moor vegetation screens the soil efficiently. Moreover, as a result of its high water content the specific heat of sedge moor soil is high and its conductivity of heat low. In the dry grassland, on the other hand, there is an absence of a dense vegetative covering. Here the soil has a low specific heat, due to its dryness, and its heat conductivity is great. Dry grassland heats up more rapidly and cools off more readily and to a greater depth sooner than either meadow or sedge moor. As regards soil temperature and soil moisture, the sedge moor shows less seasonal variation than either meadow or dry grassland. This condition appears to be correlated with the lack of marked seasonal aspects. Edaphic conditions within a community control the seasonal changes of the vegetative covering.

We have described the stages in the development of the flood plains of a mountain park. The oxbows and oxbow ponds are prominent features of these flood plains. Boulder and gravel shores or sand and fine silt shores are the initial habitats. They culminate in a temporary meadow climax. Two exceptionally distinct ages of flood plains are represented: a recently formed one now in the willow thicket stage, and an older one on the middle terrace in the meadow or temporary climax stage. A consideration of the fate of the meadow will be discussed later, after treatment of the glacial lake and dry grassland series of succession.

GLACIAL LAKE SUCCESSION

The origin of Park and Filled Lakes, the only glacial basins in Boulder Park, has been discussed. It was pointed out that these two bodies occupy the positions of two ice cores that were left on the valley floor on the retreat of the first ice mass. Immediately following the melting of these ice cores there was left a cold water lake with bare gravel and stony shores. Park Lake was formerly of much greater size; the limits of the old shore may be clearly seen on the west side of the present body of water. This filled area is now in the sedge moor stage of development, as is also Filled Lake. We may gain some idea of the early stages in the development of the shore vegetation by studying the alpine lakes which are found in abundance 6 or 8 miles west of Boulder Park. However, this difference exists: alpine lakes are comparatively well protected by cirque walls from wind effects, whereas those of Boulder Park are in the open. It is believed that this difference explains the tardy development of forest growth in the Park, and the maintenance of the temporary climax grassland.

In the lakes and ponds of Park Lake, algae are the only free floating plant life. Besides the numerous microscopic algae which constitute a portion of the plankton of these waters, *Mougeotia laetevirens* (A. Braun) Wittr. and *Spirogyra Weberi* Keutz. make up large floating masses along shores undisturbed by waves. *Anabaena flos-aquae* (Lyngbye) Breb. becomes conspicuous in late July when it appears as "water bloom" over the entire surface of the lake.

Sparganium angustifolium Michx. (fig. 11) forms a well defined aquatic community along the shore edge out to a depth of about 2 ft. It is of much importance in the aquatic successions. It grows equally well on a mud or gravelly bottom. A dwarf form occurs at the south of Park Lake on a low, flat area over which the water level fluctuates. Here the plants grow but a few inches high, and possess short, rather thick, leaves. Such plants mature fruit normally. *Callitriche palustris* L. is found in shallow water. It is most abundant where protected from wave action. *Batrachium trichophyllum* (Chaix) Bossch. is one of the first aquatics to secure a foothold in the ponds of the Park. It is the most

important aquatic in the filling process. *Potamogeton foliosus* Raf., *P. lonchites* Ruck., *P. alpinus* Balb., *P. interior* Rydb., *P. lucens* L., and *Myriophyllum spicatum* L. are other rather rare aquatics to be found here.

Aquatic plants play an important part in the life history of the lake. On the flat, mud shores the *Sparganium* association is

FIG. 11.—West shore at Park Lake; note *Sparganium* in shallow water, and zones of sedge moor and willow thicket.

immediately succeeded by the *Eleocharis-Ranunculus* community. This is well shown at the southwest shore (fig. 12). This shore is flat and gravelly or muddy, with a few small boulders scattered about. It is perennially covered with an inch or so of water up to about July 1, after which time it is a mud and gravel flat. Dwarf forms of *Sparganium angustifolium* flourish in this habitat. *Eleocharis acicularis* here, as elsewhere in such habitats, is the chief invader of the bare soil. Following close behind and upon pure tufts of *Eleocharis* come *Allocarya scopulorum* and *Alopecurus fulvus*, in the

order named. *Alopecurus* grows in caespitose clumps 3–6 inches in diameter. These tufts are the nucleus for the growth of such plants as *Epilobium Hornmannii* Reich., *Agrostis hiemalis*, and *Veronica serpyllifolia* L. Following the establishment of these herbs come *Carex variabilis*, *C. lanuginosa* Michx., *C. festiva* Dewey, *Deschampsia caespitosa*, *Phleum alpinum*, and *Poa leptocoma*. As

FIG. 12.—View of *Eleocharis-Ranunculus* association at southwest corner of Park Lake; community occupies a broad mud flat; note tufts of *Alopecurus fulvus*.

at East Lake, sedge moor may be succeeded directly by herbaceous meadow, the *Carex festiva* society being the first meadow community to become established.

Filled Lake is one of the most interesting features of the Park. This old lake bed is now in the sedge moor stage of development. The shore line is still quite distinct, made more so by the vegetative growth than by any topographic condition. Early successions now in operation at various places in the Park are undoubtedly similar to those which led up to the present sedge moor stage in Filled Lake.

The association immediately preceding the present one and the future changes are quite clear. The sedge moor is now dominated by *Carex variabilis* and *C. utriculata*, alternating and freely mixing. Obviously, *C. variabilis* has followed upon *C. utriculata*. Mosses

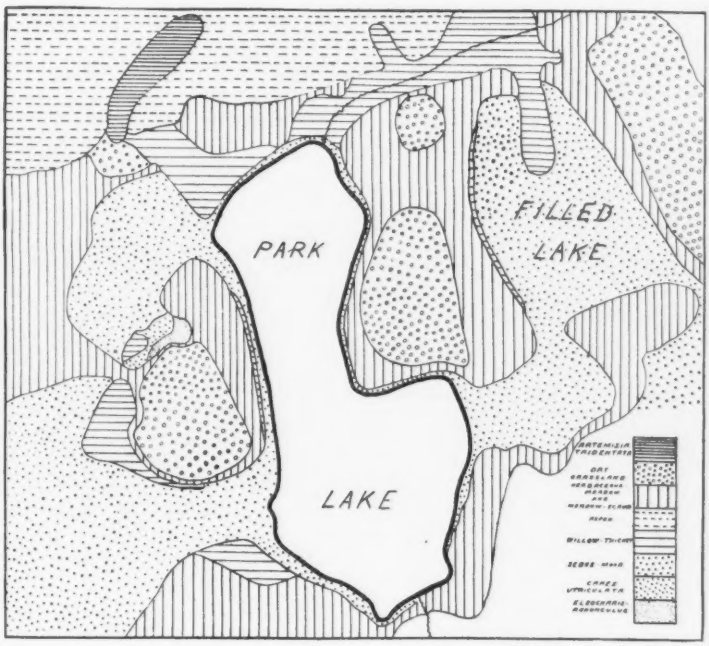


FIG. 13.—Map of Park and Filled Lakes

are an exceedingly important element in the building up of sedge moor.

If one stands at the old shore line and looks out over the flat, sedge-covered lake floor it is seen to be divided into two quite distinct parts: (1) the half nearer the outlet is lighter in color, due to the predominance of sedges, of which *C. utriculata* forms a good proportion; (2) the north half is darker, due to a pronounced admixture of *Deschampsia*, and a greater proportion of *C. variabilis* as compared with *C. utriculata*. The north half of the lake is drier.

This would be expected, since it is further removed from the outlet and is adjacent to the hill at the north, from which it has received considerable wash material.

Scattered throughout the sedge moor, and particularly in the upper half mentioned, are numerous clumps of vegetation. These are slightly elevated above the general level and vary from 1 to 3 ft. in diameter. The nucleus of a clump is usually a *Salix chlorophylla* shrub. This species is an early invader of sedge moor throughout the Park. Building in and around it are such early invaders as *Sedum rhodanthum*, *Alsine longifolia* (Muhl.) Brit., *Arabis hirsuta* Scop., *Cerastium occidentale* Greene, *Geum strictum* Ait., and *Dasiophora fruticosa*. The clumps may also originate about a

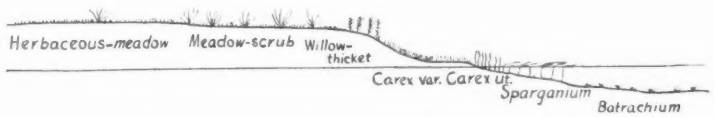


FIG. 14.—Ideal section at west shore of Park Lake

Dasiophora shrub or *Deschampsia* tuft. All the shrubs are young. Ring counts of *Dasiophora* show the large majority to be 13–15 years of age. *Salix* shrubs are older on the average. The sedge moor is rapidly being converted into meadow.

At the northwest shore of Filled Lake there is a shallow shelf extending outward from the shore line. The limits of this shelf were determined by making soil borings. These were simply used as a check on the determination of its limits by the vegetative covering. In fact, the presence of the shelf here was called to the attention by a rather marked difference in the vegetation as contrasted with that beyond. It is mentioned simply to illustrate transition conditions between sedge moor and meadow. Here *Deschampsia caespitosa* is predominant. Young *Dasiophora* shrubs are very uniformly distributed throughout. Sedges, relatively, are not an important component. Secondary species are: *Hierochloa odorata* (L.) R. and S., *Phleum alpinum* L., *Poa leptocoma*, *Cerastium occidentale*, *Alsine longifolia*, *Caltha rotundifolia* (Huth.) Greene., *Sedum rhodanthum*, *Geum strictum*, *Potentilla gracilis*, *Valeriana*

ceratophylla (Hook.) Piper, *Achillea lanulosa* Nutt., *Antennaria parvifolia* Nutt., and *Crepis perplexans* Rydb. The large number of characteristic meadow species will be noted.

The depth of the peat deposit in the lake was determined throughout. In the center it is over 10 ft. deep. From here the depth gradually decreases toward the shores. The rate of increase in depth may be judged by a set of borings made every 5 m. along an east-west line to the center of the area. Starting at the east shore this series shows depth (in cm.) as follows: 40–46–47–43–70–136–180–212–220–258–over 300.

Borings show that the lake has been filled almost entirely with the stems and leaves of *Carex*. The surface soil is loosely packed plant material, readily separated into layers, indicating seasonal deposition. The upper 6–8 inches are light brown in color; below this, the layers become darker and more compact. This soil exhibits a slight acid reaction.

It will be recalled that, at East Lake, *Salix chlorophylla* is a characteristic plant of the raised rim at the water's edge. A similar condition exists here. At the west shore there is a very distinct line of this shrub, on a more or less evident rim; at one time these formed a fringe at the water's edge. Back of this rim is a belt averaging about 20 ft. wide, clearly the old sedge moor of the lake shore. Beyond this is a meadow scrub, followed by herbaceous meadow, then dry grassland. The dry grassland is not the outcome of progressive drying of the meadow, as the zonation might suggest, but it represents a stage in a xerarch succession on the glacial gravel of the high terrace.

DRY GRASSLAND SUCCESSION

The rapid drainage of the lake which covered the entire park left a level, uniformly gravelly, area exposed to the drying and mechanical effects of the winds, and the extremes of diurnal and yearly temperatures. Lichens and *Selaginella densa* are the chief pioneers of the glacial gravels here. The latter is a mat former, and on the mats other plants gain a foothold. Its reaction upon the habitat, in holding the soil, adding humus, and retaining water, favors the entrance of such xerophytes as *Erigeron multifidus* Rydb.,

Sedum stenopetalum, *Potentilla concinna* Rich., *Carex stenophylla* Wahl., *Aragallus Lambertii* (Pursh) Greene, *Chrysopsis villosa* (Pursh) Nutt., *Comandra pallida* A.DC., *Arenaria Fendleri* Gray, *Artemisia frigida* Willd., and *A. canadensis* Michx.; simultaneously, there is an incoming of such grasses as *Muhlenbergia gracilis* Trin., *Danthonia Parryi* Scribn., *Festuca saximontana* Rydb., *Poa interior* Rydb., and *Koeleria cristata* Pers. There results a xerophytic grassland which has been designated "dry grassland." It is a persistent and long-lived plant community.

The dry grassland of Boulder Park has been the object of extended study by RAMALEY (**14, 15, 16, 17**). The association is preeminently one of coarse, gravelly, thin soils. Humus is conspicuously scarce. The soil temperatures run high throughout the vegetative season, and the soil water content low, at times falling below the wilting coefficient. The area is well exposed to the winds, and snow does not accumulate to any extent. RAMALEY has shown that 70 per cent of the most important dry grassland plants are shallow rooted, and that 33 per cent of them are rhizomatous; moreover, many of those which do not bear rhizomes have much branched caudices. Practically 91 per cent of the dry grassland plants are perennial. These facts point to the extreme xerophytism of the habitat.

The dry grassland is an open community; bare ground composes about 15 per cent of the whole area during the month of July. There is ample opportunity for seeds to find open territory; but the life of the seedling is a precarious one. There is a lack of soil water, droughts are frequent in summer, the transpiration rate is high, and there is a lack of winter snow cover. These conditions exclude the invasion of trees and many mesophytic plants.

Dry grassland has all appearances of being the ultimate vegetation throughout the Park, under present climatic and physiographic conditions at least. However, slowly but surely it is being invaded in places by meadow; a series of dry years may see the drying up of meadow, the fragmentation of plant parts, and their removal by wind, thus reinstating the dry grassland stage. The resultant is a slow encroachment of dry grassland by mesophytic grasses and other herbs. As has been indicated, if physiographic and climatic

conditions remain unchanged, the process of encroachment will be extremely slow. However, physiographic agencies are destroying the dry grassland habitat at a rate which exceeds that of biotic agencies. At many points the high terrace is being eroded by the stream, and invariably the flood plain temporarily culminates in meadow; again, débris is accumulating at the bases of slopes and in the depressions between glacial hummocks. On this fine grained and deeper soil, with its greater water retentiveness, meadow species become well established; hence it is seen that the combined activities of biotic and physiographic factors are resulting in the slow disappearance of the dry grassland and the establishment thereupon of a mesophytic grassland. FULLER (6) points out that whereas the hydrarch succession of Boulder Park is closely comparable to that of the Illinois prairie, the Park area exhibits a xerarch succession comparable to nothing found in Illinois.

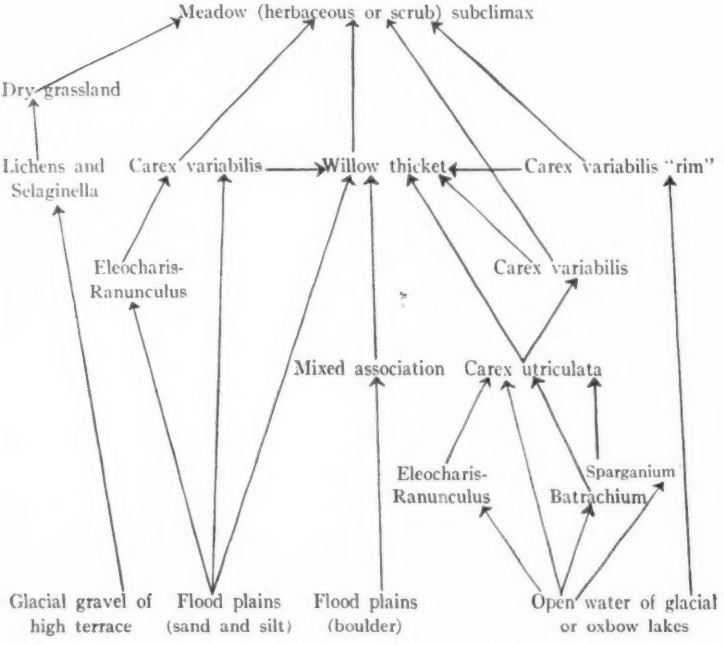
Two types of meadow are displayed in the Park which we have designated "herbaceous meadow" and "meadow scrub." The latter consistently occupies moister situations, and very frequently precedes herbaceous meadow in the succession.

The seasonal aspects and detailed structure of the meadow need not be entered into extensively here. REED (21) has given us a report of the chief meadow societies in the Park, together with a list of the meadow plants with their frequency and soil moisture index.

Carex festiva forms distinct meadow societies on the middle terrace and about the lakes. Where the slope of the lake shore is gradual, sedge moor immediately joins on to this society. Its chief associates are *Deschampsia caespitosa*, *Phleum alpinum*, *Potentilla gracilis* Dougl., *Poa Buckleyana* Nash, and *Poa pratensis* L. A conspicuous society of *Pedicularis Parryi* Gray occurs just outside the *Carex festiva* society in soil that is drier and more shallow. A quadrat census of the plants of the society showed the principal species to be *Potentilla gracilis*, *Astragalus alpinus* L., *Pseudocymopterus sylvaticus* A. Nels., and *Chondrophylla Fremontii* (Torr.) A. Nels. The most unobservant person would remark about the well defined limits of the *Pentstemon procerus* Dougl. society. It extends in a semicircle about the south flank of a low,

morainal elevation on the east side of Park Lake, and is also characteristic of glacial sinks. Grasses do not form a close growth, but other herbaceous species predominate. *Troximon glaucum* Nutt., *Potentilla gracilis*, and *Valeriana edulis* Nutt. are the principal associates. A society, the main representatives of which are

DIAGRAM OF PLANT SUCCESSION, BOULDER PARK, COLORADO



Erigeron macranthus Nutt., *Campanula Parryi* Gray, and *Eriogonum subalpinum* Greene, is characteristic of the meadow that immediately adjoins dry grassland. Associated species are *Galium boreale* L., *Achillaea lanulosa* Nutt., *Stipa Nelsonii* Scribn., *Poa interior* Rydb., and *Koeleria cristata* (L.) Pers.

Discussion

Based upon the water content of the initial habitat, the successions may be classified as hydrarch and xerarch. The hydrarch

succession involves the glacial lakes, and the flood plains with deposition banks of silt and sand; the xerarch succession involves the gravels laid bare by the rapid drainage of a glacial lake which at one time occupied the greater part of the Park, and the flood plains with shores of coarse gravel or shingle. The stages in these series lead to a temporary meadow climax (subclimax). The climax is reached much sooner by the hydrarch than by the xerarch series. In fact, much of the high terrace is now in the dry grassland stage, which under existing environmental conditions, incident to the topographical setting of the Park, promises to be long standing. However, there is ample evidence that even under these circumstances it is being slowly replaced by meadow. Moreover, the physiographic operations now in progress, namely, the erosion of Boulder, Meadow, and Trestle Creeks, and the accumulation of wash material at the bases of slopes, look toward the disappearance of the dry grassland habitat and the ushering in of meadowland.

The question now arises, are trees advancing upon the meadow? The forest associations bordering the Park are as follows: (1) aspen (*Populus tremuloides* Michx.), (2) lodgepole pine, (3) (*Pinus Murrayana* Oreg. Com.), and (3) *Engelmann spruce-subalpine fir* (*Picea Engelmannii* [Parry] Engelm.—*Abies lasiocarpa* [Hook.] Nutt.). Aspen often forms a fringe between the coniferous associations and the meadow of the open Park. This relation prevails throughout the Rocky Mountain region. Wherever the developmental series has led up to the meadow stage, however, as it has in Boulder Park, this stage bids fair to hold its ground against the invasion of trees, thus constituting a climax (subclimax) of long duration. The principal factor involved here is competition. It may occur to one that, although the competition of meadow species prevents the forestation of the open Park, there is nothing to prevent the dry grassland with its abundance of open ground being invaded by trees. In this connection it may be said that the exposure of the dry grassland to excessive evaporation as conditioned by wind, temperature, and the lack of a snow cover makes a situation in which trees find it impossible to get a start. The climatic climax of the region is a forest of Englemann spruce-subalpine fir.

In comparing the mountain lakes with those of the plains and lower altitudes generally, it is striking that those of lower elevations support the richer aquatic vegetation. The ponds of Boulder Park do not have many species commonly known as belonging to the water habitat. For example, there will be noted the total absence of species of *Lemna*, *Hydrocharis*, *Ceratophyllum*, *Utricularia*, *Riccia*, *Azolla*, and *Salvinia*, free floating species common at lower altitudes. Of these, several *Lemna* spp. and *Utricularia vulgaris* have been collected at elevations in Colorado as high as Boulder Park. Many submersed and emersed fixed species are not to be found here. Among such may be mentioned species of *Nitella*, *Isoetes*, *Naias*, *Elodea*, *Nymphaea*, and a number of *Potamogeton* spp. Several other species of *Potamogeton*, *Nymphaea polysepala* (Engelm.) Greene, *Isoetes Bolanderi* Engelm., *I. paupercula* (Engelm.) A. A. Eaton, and *Naias gaudalupensis* (Spreng.) Morong are reported from a few lower altitudes in Colorado.

The scarcity of aquatic plant life in the lakes and ponds of the Park is in part due to the coldness of the waters during a considerable portion of the year. Moreover, the marsh type of vegetation here is meager, and little shelter is offered to many free floating forms. The lakes and ponds in Boulder Park contain very soft water. No doubt the same is true of most high altitude lakes. Nearly all plains lakes, however, are rich in alkali salts; bicarbonates of calcium and magnesium, also of potassium and sodium, are quite universally present. A number of workers (**2, 5, 25**) have noted that waters rich in lime carbonates have a richer aquatic flora and fauna than soft waters. In the absence of free carbon dioxide, water plants may make use of the half-bound carbon dioxide of bicarbonates, chiefly those of calcium and magnesium, dissolved in the water. Undoubtedly the kind and quantity of dissolved salts in lake waters is an important factor in controlling vegetative development. In Boulder Park lakes and ponds the absence of these salts is quite likely a most important factor limiting the growth of algae and other submerged aquatics.

The total absence of *Scirpus*, *Typha*, and *Phragmites* reed swamps in Boulder Park will be noted.

SPHAGNUM BOGS.—Sphagnum moss is found in very small amounts here and there in the Park, but in no place is there any approach to the formation of sphagnum moor. Small sphagnum moors are occasionally found at higher elevations in heavily forested areas in northern Colorado, but never are they as well developed and characteristic as those found north and east in the United States.

For the optimum development of sphagnum, there must be abundant precipitation, slow evaporation from the surface, slow percolation and run-off of soil water, low temperature, and absence of drying winds. In only favored situations are such conditions found in Colorado. Boulder Park is a very unfavorable locality for the development of sphagnum moors. Here the drainage is generally good, the temperatures of both air and soil may run high, at least for a short period, many seasons are dry, and the winds are desiccating. In his description of the bog plant societies of northern North America, TRANSEAU (**24**) has selected 15 characteristic bog plants: *Menyanthes trifoliata*, *Dulichium arundinaceum*, *Comarum palustre*, *Scheuchzeria palustris*, *Eriophorum polystachon*, *Drosera rotundifolia*, *Sarracenia purpurea*, *Oxycoccus oxycoccus*, *Chiogenes hispidula*, *Andromeda polifolia*, *Chamaedaphne calyculata*, *Ledum groenlandicum*, *Kalmia glauca*, *Betula pumila*, and *Larix laricina*. Of these, *Eriophorum polystachyon* is the only one found in Boulder Park, and it is rare. *Menyanthes trifoliata* has been found in a bog a number of miles north of Boulder Park.

The writer is indebted to Dr. H. C. COWLES, under whom this study was conducted, for his helpful suggestions and criticisms; to Professor FRANCIS RAMALEY for valuable advice and for laboratory facilities granted at the Mountain Laboratory for Field Biology (Tolland, Colorado); to Professor AVEN NELSON, who identified a large number of the specimens; and to Mr. A. S. HITCHCOCK for the identification of some difficult species of *Poa*.

STATE AGRICULTURAL COLLEGE
FORT COLLINS, COLO.

LITERATURE CITED

1. ATWOOD, W. W., The glaciation of the Uinta Mountains. Jour. Geol. **15**:790–804. 1907.
2. BIRGE, E. A., and JUDAY, C., The inland lakes of Wisconsin; dissolved gases and their biological significance. Wis. Surv. Bull. 22. 1911.
3. BRUDERLIN, KATHERINE, A study of the lodgepole pine forests of Boulder Park, Tolland, Colo. Univ. Colo. Studies **8**:265–275. 1911.
4. CAPPS, S. R., and LEFFINGWELL, E. D. K., Pleistocene geology of the Sawatch Range near Leadville, Colo. Jour. Geol. **12**:698–706. 1904.
5. CHAMBERS, C. O., The relation of algae to dissolved oxygen and carbon dioxide with speciall reference to the carbonates. 23d Ann. Rep. Mo. Bot. Gard. 171–207. 1912.
6. FULLER, G. D., A comparison of certain Rocky Mountain grasslands with the prairie of Illinois. Trans. Ill. Acad. Sci. **8**:1–10. 1917.
7. GWILLIM, J. C., Glaciation in the Atlin district, British Columbia. Jour. Geol. **10**:182–186. 1902.
8. HERSHEY, O. H., The relation between certain river terraces and the glacial series in Northwestern California. Jour. Geol. **11**:431–459. 1903.
9. JEFFERSON, W. D., A certain type of lake formation in the Canadian Rocky Mountains. Jour. Geol. **7**:247–261. 1899.
10. RAMALEY, FRANCIS, Plant zones in the Rocky Mountains of Colorado. Science N.S. **26**:642–643. 1907.
11. ———, Botanical opportunity in Colorado. Univ. Colo. Studies **6**:5–10. 1908.
12. ———, The University of Colorado Mountain Laboratory. Univ. Colo. Studies **7**:91–95. 1909.
13. ———, Northern Colorado plant communities with special reference to Boulder Park. Univ. Colo. Studies **7**:223–236. 1910.
14. ———, The amount of bare ground in some mountain grasslands. BOT. GAZ. **57**:526–528. 1914.
15. ———, The relative importance of different species in a mountain grassland. BOT. GAZ. 60:154–157. 1915.
16. ———, Quadrat studies in a mountain grassland. BOT. GAZ. **62**:70–74. 1916.
17. ———, Dry grassland of a high mountain park in Northern Colorado. Plant World **19**:249–270. 1916.
18. RAMALEY, FRANCIS, and MITCHELL, L. A., Ecological cross-section of Boulder Park (Tolland, Colo.). Univ. Colo. Studies **8**:277–287. 1911.
19. RAMALEY, FRANCIS, and ROBBINS, W. W., A summer laboratory for mountain botany. Plant World **12**:105–110. 1909.
20. ———, Studies in lake and streamside vegetation. I. Redrock Lake near Ward, Colo. Univ. Colo. Studies **6**:1. 1909.

21. REED, E. L., Meadow vegetation in the montane region of Northern Colorado. Bull. Torr. Bot. Club **44**:97–109. 1917.
22. ROBBINS, W. W., Native vegetation and climate of Colorado in their relation to agriculture. Colo. Agric. Exper. Sta. Bull. **224**:1–56. 1917.
23. SALISBURY, R. D., and BLACKWELDER, E., Glaciation in the Bighorn Mountains. Jour. Geol. **11**:216–223. 1903.
24. TRANSEAU, E. N., On the geographical distribution and ecological relations of the bog plant societies of Northern America. BOT. GAZ. **36**:401–421. 1903.
25. WESENBERG-LUND, Comparison of Scottish with Danish lakes. Revue Hydrobiol. **1**:184–187. 1908.
26. WESTGATE, L. H., The Twin Lakes glaciated area, Colorado. Jour. Geol. **13**:285–312. 1905.

QUANTITATIVE MEASUREMENT OF PERMEABILITY

WALTER STILES AND INGVAR JØRGENSEN

OSTERHOUT (**8**) has recently sought to explain the divergent results of some of his experiments and some of our own, on the basis of our confusion of permeability with absorption. It seems to us that any confusion that may have arisen is due largely to the different interpretations placed by different workers on such expressions as permeability in relation to complex systems like the cell. In this paper we discuss especially the meaning of the term permeability when it is used in a quantitative sense, and at the same time we take the opportunity of dealing with the points raised by OSTERHOUT in regard to the relation of his results and conclusions with our own. The term permeability may be classed with those expressions in current use in plant physiology which BARNES and LIVINGSTON (**4**) have described as cloaks for our ignorance. We may vaguely understand what is meant by the permeability of a membrane in regard to a particular substance, that is, its capacity for allowing the substance to pass through the membrane, although we may have no very clear idea as to how this takes place. In the case of the living cell, however, the matter is not so simple.

The nomenclature used in regard to the passage of substances into and out of the living cell has largely resulted from the work of DE VRIES on plasmolysis, and the theory derived from his results. It is a matter of common knowledge that as a result of the researches of DE VRIES (**17, 18**) and PFEFFER (**9, 10**), the plant cell came to be practically universally regarded as an osmotic cell, a solution surrounded by a semipermeable membrane, the plasma membrane, constituting the outer layer of the protoplast. On this view the permeability of the plasma membrane obviously means its capacity for allowing a substance to pass through the membrane. As plant physiology has developed, however, the realization of the complexity of the systems with which the plant physiologist has to deal has become more and more general, and it must be admitted that such a simple theory as that of DE VRIES will not afford a complete

explanation of the facts. Indeed, DE VRIES himself realized something of the complexity of the system, for he lays emphasis on the presence of two membranes which function in permeability phenomena, the outermost layer of the protoplasm, the plasma membrane, and the layer separating the rest of the protoplasm from the vacuole, the vacuole wall.[1]

In the simplest case of a plant cell immersed in a solution we have four phases: the external solution, the cell wall, the protoplast, and the vacuole; and in addition there are the limiting layers between these various phases which may have properties differing from those of either phase. We may represent such a system by the following scheme:

external solution	cell wall	protoplast	vacuole
phase boundary	phase boundary (plasma membrane)	phase boundary (vacuole wall)	

Again, in plant tissue intercellular spaces may also affect the results of investigations. Obviously in dealing with such a complex system the term permeability used in regard to the cell should only be used as a general expression to cover the various phenomena concerned in the passage of substances between living tissue and the external medium or between cell and cell in the living organism. It is in this sense that we have used the term permeability in our series of papers on these questions in *Annals of Botany;* we do not mean the capacity of substances to pass through any one particular phase of the system.

The permeability of living cells being then such a complex matter, it seems advisable not to use such expressions as "permeability coefficient," "measure of permeability," and "temperature coefficient of permeability," unless it is made clear what part of the system it is whose permeability is being considered. In our opinion the only legitimate use of such expressions is when they refer to the passage of substances into and out of the cell, or between one cell and another. Generally it is impossible by the methods of

[1] Cf. PFEFFER (II, p. 90): "In order to reach the cell sap a particle of water or dissolved substance must diosmose first through the cell wall and the plasmatic membrane which is closely applied to it, and finally pass through the internal limiting plasmatic membrane, which bounds the vacuole."

investigation at present available to analyze further the behavior of substances in passing through the various phases or across the boundaries between them. Hence, when we have used the term permeability in a quantitative sense we mean simply the capacity of a substance for entering the cell from the outside, or of passing out from the cell into the external medium, which are the phenomena with which we have so far mainly dealt. Generally we have not used the term permeability at all in a quantitative sense. Wherever possible it is much better to use the terms absorption or exosmosis, as the case may be, which have a definite unmistakable meaning and whose meaning does not depend upon an unproved and imperfect theory as does the term permeability as used by some writers.

In a paper (**14**) which appeared three years ago, we published the results of some experiments from which we concluded that the relation between time and absorption of hydrogen ions by potato cells was a logarithmic one, and that the temperature coefficient of this absorption was about 2.2. From this result it was pointed out that "the study of the effect of temperature on the absorption of the hydrogen ion would seem to indicate that this absorption is controlled by some chemical action in the cell, and is not the result of simple diffusion through the plasma membrane or of mere adsorption by the cell protoplasm." When therefore OSTERHOUT (**8**) says "it is evident, therefore, that the temperature coefficient observed by STILES and JØRGENSEN may be that of a chemical process involving the union of hydrogen ions with some constituent of the cell other than the plasma membrane," so far from contradicting our statement he is merely repeating our own conclusion in not very different words. When, however, he continues, "in which case it would have no bearing upon the problem of the nature of permeability," it would appear that he uses the term permeability, not in the general sense which we regard as the only legitimate one in which it can be used without qualification, but in a restricted sense, namely, the capacity of hydrogen ions for passing through "the plasma membrane (or other surface)." Against this restricted use of such a commonly used term as permeability we would enter a protest, as it rests upon a theory

which is unproved, which at best must be incomplete, and from which indeed many workers now dissent (FISCHER **1**, MOORE, ROAF, and WEBSTER **5, 6**). When, therefore, OSTERHOUT says of us that "they regard the temperature coefficient found by them as the temperature coefficient of permeability to hydrogen ions," he is completely misrepresenting our views on the matter. We never used the expression "temperature coefficient of permeability" for the reasons already mentioned, but if we had done so, we should certainly not have used the term permeability in the restricted sense in which OSTERHOUT appears to use it.

We may point out that OSTERHOUT's conclusion that we regard the temperature coefficient found by us as the "temperature coefficient of permeability" is based on the following assumptions: (1) that we "apparently reach the conclusion that 'the substance with which the acid reacts' is 'presumably the plasma membrane or some part of it'"; (2) that we support the view of PAULI and SZÜCS that the entrance of ions into the cell is due to the reversibility of a reaction between ions and the plasma membrane; (3) the title of our paper "The effect of temperature on the permeability of plant cells to the hydrogen ion." With regard to the first statement, we neither apparently nor in reality reached that conclusion. What we actually said was that our results indicated "that the quantity of substance with which the acid reacts, presumably the plasma membrane, or some part of it, remains constant as it does not influence the rate of the reaction." This is quite a different statement. We said "presumably the plasma membrane" because it could not be assumed that it was the plasma membrane;[2] it might be any part of the cell. It is quite an immaterial point; our argument holds equally whether the action takes place in the limiting layer or elsewhere in the cell.

Again, OSTERHOUT's second statement that we support the view of PAULI and SZÜCS is not founded on fact. We actually said, "this *suggests* that *either* the absorbing substance is present in such

[2] The term "plasma membrane" is another of those semimystical expressions whose use does not help in the elucidation of scientific problems. We prefer to use this expression in the way that LEPESCHKIN uses it, simply as meaning that part of the cell where the permeability phenomena are taking place. Compare our recent remarks on this term (**15**).

large quantity as compared with the acid that the amount changed is small in comparison with the total amount, *or* that the substance formed as a result of the absorption is broken down again almost as soon as formed. Such a view of the plasma membrane is held by PAULI and SZÜCS, who regard the entrance of ions into the cell as due to the reversibility of such a reaction between ions and the plasma membrane. *We feel, however, that more experimental evidence is required before such theories can be discussed adequately and with profit.*" It is extraordinary that anyone could see support for SZÜCS's view in that statement.

Finally, in the title of the paper the term permeability was used in its ordinary general sense, and in our opinion the title gave a reasonable representation of the contents of the paper, which should be its function.

For the reasons already stated we hold that that large body of workers who have included the absorption or exosmosis of dissolved substances among the phenomena of permeability are completely justified. OSTERHOUT's statements, "the results obtained by these methods have been so largely misinterpreted," and "the principal difficulty lies in confusing permeability with absorption" seem to be due to his giving to the term permeability an indefinite and yet restricted meaning. It is unfortunate that he should not have realized that he and the writers he criticizes use the word permeability in a different sense; it is still more unfortunate that he should attribute to them his own use of the term permeability, and it is particularly regrettable that he should assume they mean the same things by "temperature coefficient of absorption" and "temperature coefficient of permeability" (in his sense, not theirs) when they carefully avoid such an expression as "temperature coefficient of permeability" on account of its indefinite meaning.

OSTERHOUT says that he himself used a method for determining the temperature coefficient of permeability which is free from the "objections" just discussed. We may now consider how far this statement is justified. He states that "by this method the electrical conductivity of living tissue was determined in such a way that it may be regarded as a measure of the permeability of the protoplasm." We propose therefore to discuss OSTERHOUT's work under

three heads: (1) which part of the system it is, the permeability of which he intends to measure; (2) how far the values he obtains for the electrical conductivity of plant tissues are true measures of this conductivity; and (3) whether it is legitimate to assume that the electrical conductivity is a measure of the permeability.

In regard to the first question it is perhaps significant that when discussing the statements of the writers OSTERHOUT should speak of permeability in reference to the passage of substances through "the plasma membrane (or other surface)," while when discussing his own he should refer to the "permeability of the protoplasm." It is therefore not at all clear what it is that OSTERHOUT considers he is measuring, whether he is dealing with the whole cell content or part of it, or only the limiting layer of the protoplasm.

We come then to OSTERHOUT'S method of measuring the electrical conductivity of living tissues. The essential of this method (**7**) is that a pile of disks of *Laminaria* thallus is immersed in sea water or other medium between two electrodes. These are separated by a length of 20 mm. of sea water and the resistance between them measured. This resistance is called the resistance of the apparatus. The electrodes are then separated so that the roll of *Laminaria* disks is inserted between the electrodes in such a position that between each end of the roll of disks and the electrode is a length of 10 mm. of sea water. The resistance is again measured and the increase in resistance is taken to be the resistance of the tissue. Now whether the resistance of the tissue can be determined in this way depends entirely upon the form of the apparatus used, for the 20 mm. of sea water and the tissue must be strictly in series and there must be no surrounding conductor through which current might pass. As OSTERHOUT has never published any details regarding the arrangement of his apparatus, it is impossible to accept his results when their correctness is highly dependent upon the details of the experimental arrangement. Indeed, certain facts given in OSTERHOUT'S very inadequate description suggest an incorrect arrangement; for instance, why, if the sea water and *Laminaria* are arranged in series, should the resistance of 2 cm. of sea water be 305, while the resistance of 2 cm. of sea water plus a cylinder of sea water of the same transverse dimensions as the

tissue (5 cm. long) is only 392? No doubt an explanation of this is forthcoming, but it has not been given so far, and it will serve to indicate the necessity for a full description of OSTERHOUT'S apparatus and method before his conductivity measurements of tissues can be accepted by other workers.

Finally, there is the question as to whether the electrical conductivity of tissue can be used as a measure of permeability. Can it be assumed that the electrical conductivity as measured by KOHLRAUSCH'S method is really a measure of the permeability of the protoplasm to ions? We have already called attention (**12, 13**) to the fact that the conductivity of tissue is the resultant of the conductivity of a variety of different phases, and owing to the complex arrangement of these phases it cannot be assumed that the conductivity of the whole is the sum of the conductivity of each phase. HÖBER (**2, 3**), using a method which it is true is perhaps not above criticism, comes to the conclusion that the interior of the cell only contributes relatively slightly to the total conductivity. Moreover, OSTERHOUT neglects the fact that if the penetrability for ions increases, a necessary consequence of this may be increased diffusion between the external medium and the interior of the tissue, resulting in changes of concentration in the interior of the cell. Similarly, any change which altered the concentration or the distribution of free electrolytes in the interior of the cell would alter the conductivity. It may be, although we do not certainly know, that electrical conductivity gives a rough idea of the permeability of the cell; it is extremely unlikely that it gives numbers so exactly proportional to any kind of permeability that "temperature coefficients of permeability" can be calculated from them. Hence we consider it impossible to accept any of OSTERHOUT'S results obtained by his electrical conductivity method with *Laminaria* disks until (1) he makes clear what he means by permeability when this word is used in a quantitative sense; (2) he has given proof that his method does give values for the electrical conductivity of the tissue employed; and (3) he has produced evidence that the electrical conductivity of tissue can be taken as a measure of permeability in the sense in which he uses that word.

We should also like to raise two further points arising out of OSTERHOUT'S work. In the first place, we would point out that in

his discussion of our results, he would apparently apply conclusions derived from a brown alga immersed in a strong salt solution (about $\frac{N}{2}$), to potato tuber immersed in a dilute acid solution $\left(\frac{N}{1000}\right)$. Such a method of argument seems to us illegitimate. It is not to be accepted as a first principle that the permeability of every tissue, and permeability in regard to every substance or ion, will follow the same law. Secondly, we should like to caution in regard to temperature coefficients. When the temperature coefficient of the absorption of water by one tissue is found to be about 1.3 and by another tissue 3.0, as we have found with carrot and potato respectively, it should make one hesitate to draw conclusions as to the nature of a reaction from the magnitude of its temperature coefficient. That the temperature coefficient of the absorption of hydrogen ions by potato tissue is about 2.2 suggests, as we said previously, that the absorption is controlled by a chemical action, but without further evidence it is not more than a suggestion. This is forthcoming from the shape of the time-absorption curve and the fact that the absorption of hydrogen ions continues long after the concentration of hydrogen ion inside the tissue would be greater than that outside if no chemical action took place.

It must also not be forgotten that in cell problems we are dealing with a complex heterogeneous system, with probably a number of related and interdependent actions taking place, each one of which may have a different temperature coefficient. It would not be in any way surprising to obtain different coefficients for the same complex of processes with tissue that had had a different previous history, as we point out in a recent paper (**16**).

In conclusion, we should like to enter a plea for definiteness of statement and for the avoidance of semimystical expressions such as "permeability" or "plasma membrane" used in a quantitative and yet undefined sense. Above all, should be avoided the drawing of conclusions and the putting forward of theories on insufficient data.

IMPERIAL COLLEGE OF SCIENCE AND TECHNOLOGY
LONDON

LITERATURE CITED

1. FISCHER, M., Œdema, a study of the physiology and the pathology of water absorption by the living organism. New York. 1910.
2. HÖBER, R., Ein zweites Verfahren, die Leitfähigkeit in Innern von Zellen zu messen. Pflügers Arch. Gesam. Physiologie **148**:189–221. 1912.
3. ———, Messungen der innern Leitfähigkeit von Zellen. Dritte Mitteilung. Pflügers Arch. Gesam. Physiologie **150**:15–45. 1913.
4. LIVINGSTON, B. E., A quarter century of growth in plant physiology. Plant World **20**:1–15. 1917.
5. MOORE, B., and ROAF, H. E., Direct measurements of the osmotic pressure of certain colloids. Biochem. Jour. **2**:34–73. 1907.
6. MOORE, B., ROAF, H. E., and WEBSTER, T. A., Direct measurement of the osmotic pressure of casein in alkaline solution. Experimental proof that apparent impermeability of a membrane to ions is not due to the properties of the membrane but to the colloid contained within the membrane. Biochem. Jour. **6**:110–126. 1912.
7. OSTERHOUT, W. J. V., Über den Temperatur Koeffizenten des elektrischen Leitvermögens im lebenden und toten Gewebe. Biochem. Zeitsch. **67**: 273–276. 1914.
8. ———, Does the temperature coefficient of permeability indicate that it is chemical in nature? BOT. GAZ. **63**:317–320. 1917.
9. PFEFFER, W., Osmotische Untersuchungen. Leipzig. 1877.
10. ———, Zur Kenntnis der Plasmahaut und der Vacuolen. Abh. Sächs. Gesell. Wiss. **16**:187–343. 1890.
11. ———, The physiology of plants (English trans.). Vol. 1. Oxford. 1900.
12. STILES, W., and JØRGENSEN, I., The measurement of electrical conductivity as a method of investigation in plant physiology. New Phytol. **13**: 226–242. 1914.
13. ———, Studies in permeability. I. The exosmosis of electrolytes as a criterion of antagonistic ion action. Ann. Botany **29**:340–367. 1915.
14. ———, Studies in permeability. II. The effect of temperature on the permeability of plant cells to the hydrogen ion. Ann. Botany **29**:611–618. 1915.
15. ———, Studies in permeability. IV. The action of various organic substances on the permeability of the plant cell, and its bearing on Czapek's theory of the plasma membrane. Ann. Botany **31**:47–76. 1917.
16. ———, Studies in permeability. V. The swelling of plant tissue in water and its relation to temperature and various dissolved substances. Ann. Botany **31**:415–434. 1917.
17. DE VRIES, H., Eine Methode zur Analyse der Turgorkraft. Jahrb. Wiss. Bot. **14**:427–601. 1884.
18. ———, Plasmolytische Studien über die Wand der Vacuolen. Jahrb. Wiss. Bot. **16**:465–598. 1885.

THE ZOOCECIDIA OF NORTHEASTERN UNITED STATES AND EASTERN CANADA

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 239

B. W. WELLS

This summary is based upon a completed descriptive account[1] of the zoocecidia of the region studied, which is that phytogeographic region dealt with by GRAY'S *New Manual of Botany* (7th ed., 1908). The only similar general statement preceding this is that of FELT (**4**), who has presented some approximate figures from an entomological standpoint pertaining to American insect galls. The mite (Eriophyidae) galls were not included in his discussion.

Historical

Three local studies of zoocecidia have been made which deserve mention in a brief historical account. COOK (**2**) in 1904 published the description of 66 galls from Indiana. JARVIS (**7**) in 1908 presented a catalogue of the insect galls of Ontario, comprising 221 species. STEBBINS (**10**) in 1910 described 205 species of galls collected in the vicinity of Springfield, Massachusetts. A posthumous catalogue of 233 southern New England galls by THOMPSON (**11**) appeared in 1915, edited by FELT. This also included a summary of American Cynipidae galls, listing 350 species.

For the sake of comparison a short summary of the European work will be given. HAIMHOFFEN (**5**) in 1858 presented 350 as the number of zoocecidia for central Europe. SCHLECHTENDAL (**9**) in 1891 listed 1315 insect, mite, and nematode galls on the plants of Germany. KIEFFER (**8**) in 1901 published a synopsis of the zoocecidia of Europe. There also appeared the same year a more exhaustive study in DARBOUX and HOUARD'S (**3**) systematic

[1] The work contains the description of 792 nematode, mite, and insect galls; half of this number will be supplemented by illustrations. Keys to the galls on the various plant genera have been made, the plant genus constituting the unit by which the galls have been grouped.

catalogue of the zoocecidia of Europe and the basin of the Mediterranean, a work which in 1908 (supplement 1913) was expanded by HOUARD (**6**) into the largest systematic cecidological work in existence. This final general European work comprises the description of 1950 zoocecidia.

Basis and plan of work

The data from which the following summary is drawn were obtained during a period of 4 years, in which field studies in Connecticut, Ohio, and Kansas were supplemented by a thorough canvass of the highly scattered cecidological literature.

It may be of interest to mention the simple and, it is believed, practical scheme which has been followed in the arrangement of the 792 types described. The plant genus was made the unit under which the galls were grouped. This is in contrast to HOUARD'S plan; he used the species, a plan which necessitated a vast amount of repetition, since innumerable galls occur on more than one species within the genus. It is a striking fact that very few galls are found upon more than one genus. In the study of the galls of the northeastern United States, data concerning the plant species bearing the gall have been included with the descriptive material. To assist in locating the descriptions, keys were worked out for the genera having more than 6 or 8 species. A brief bibliography presenting the most important references was appended to each description.

The plant genera in the work have been arranged alphabetically. The galls under each genus have been aggregated according to the classification of the cecidozoons. It is thus evident that artificial classification has been pursued throughout. At the present time any classification of zoocecidia must be artificial. The morphological data available, particularly of an anatomical nature, are far too meager to make possible anything approaching a natural classification.

Summary of numerical data

In the case of all of the following figures presented, it should be understood that they are but approximations. So new is the field of systematic zoocecidology in America, and so incomplete and

unsatisfactory are the data in innumerable specific instances, that at the present time any generalizations of a numerical nature cannot be accepted as expressing the exact condition.

A tabulated statement of the 792 galls known from the northeastern quarter of the United States and eastern Canada, according to the cecidozoon orders and families, is as follows:

DISTRIBUTION BY ANIMAL FAMILIES

Nematoidea (Nematohelminthes)		Gelechiidae	3
Anguillulidae	2	Elachistidae	2
Acarida (Acarina)		Sesiidae	1
Eriophyidae	87	Tortricidae	2
Hemiptera (Insecta)		Unclassified	10
Aphididae	70	Diptera	
Psyllidae	6	Trypetidae	7
Jassidae	1	Itonididae	383
Coleoptera		Hymenoptera	
Cerambycidae	2	Chalcidae	2
Buprestidae	1	Tenthridinidae	13
Lepidoptera		Cynipidae	194
Tineidae	1		

As FELT has pointed out, the family containing the most gall makers is the Itonididae, embracing in our region 47 per cent of the gall biota. The Cynipidae follow with 37 per cent. The other families are represented by much smaller percentages, the Coleoptera being barely represented with 3 ill-defined galls.

The distribution of the galls (except nematode) by the plant families on whose members they occur is as follows. The families are arranged in the sequence given in GRAY'S *Manual*.

DISTRIBUTION BY PLANT FAMILIES

Pinaceae	13	Aristolochiaceae	2	Rosaceae	70
Typhaceae	1	Polygonaceae	2	Leguminosae	18
Gramineae	5	Chenopodiaceae	5	Euphorbiaceae	4
Cyperaceae	1	Nyctaginaceae	1	Anacardiaceae	10
Juncaceae	1	Portulacaceae	1	Aquifoliaceae	1
Liliaceae	9	Ranunculaceae	7	Celastraceae	1
Iridaceae	1	Magnoliaceae	2	Aceraceae	14
Salicaceae	60	Lauraceae	5	Balsaminaceae	3
Juglandaceae	64	Papaveraceae	1	Rhamnaceae	2
Betulaceae	18	Cruciferae	1	Vitaceae	20
Fagaceae	183	Saxifragaceae	5	Tiliaceae	7
Urticaceae	37	Hamamelidaceae	7	Malvaceae	1

DISTRIBUTION BY PLANT FAMILIES—*Continued*

Hypericaceae	2	Ericaceae	17	Labiatae	14
Violaceae	2	Primulaceae	1	Solanaceae	3
Cactaceae	1	Ebenaceae	2	Scrophulariaceae	2
Lythraceae	1	Oleaceae	6	Bignoniaceae	1
Onagraceae	1	Apocynaceae	1	Rubiaceae	3
Araliaceae	1	Asclepiadaceae	2	Caprifoliaceae	10
Umbelliferae	1	Convolvulaceae	1	Compositae	121
Cornaceae	11	Verbenaceae	3		

The striking fact brought out by this list is the extreme irregularity of the distribution. Many of the larger families have few or no galls, while on the other hand a few of the smaller families, particularly the Fagaceae, possess many cecidia. *Quercus* alone has 176 galls, of which 157 are cynipid types. FELT presents 277 as the approximate figure for the cynipid galls on the American oaks. The Cynipidae-Quercus situation in Europe as well as in America presents the most striking example of gall evolution within a single genus of plants related to a comparatively few (9 or 10) closely related genera of insects.

It is worthy of note that such large families as the Caryophyllaceae, Cruciferae, and Boraginaceae contain no gall-bearing species. The Umbelliferae possess but a single gall. The widely distributed tree species *Platanus occidentalis* does not bear any zoocecidia.

The problem in distribution on the plants presented by the preceding list is an exceedingly difficult one and probably cannot be answered on the basis of the physiological information at present available. This intimate and constant relation between specific insects and specific plants forms one of the most significant phenomena in the field of cecidology.

As far as data were obtainable, figures were worked out indicating the distribution of the galls on the plant parts, with the following result:

DISTRIBUTION ON PLANT PARTS

On leaf blade (of these 52 are "blister" galls)	427	On roots	12
On petiole (most of these occur also on blade)	47	On flowers	27
On stem (8 per cent of these occur also on the leaf)	208	From buds forming a rosette type	47
		From buds forming a solid concentric type	30

Slightly over half of the galls (53 per cent) occur on the leaf blade. This fact is of course related to the relatively large amount of embryonic leaf tissue exposed in the early stages of shoot development. In the cases of the stem, root, and bud galls numerous factors enter, but perhaps the most important is the factor of insect equipment necessary to place the larval cecidozoon in contact with the meristematic tissues.

Some figures pertaining to gall structure were obtained which are of interest. A few words of explanation are necessary before presenting the tabulation. Under the monothalamous galls were included those types which, so far as could be determined, are generally one-chambered, that is, the gall never is a structure constantly characterized by the confluence of the walls of two or more chambers as in the polythalamous condition. A few species are intermediate and were classified in the direction in which it was believed they leaned the more strongly. A number of galls, such as the erineum (hypertrophied epidermal cells) types, do not fall in either of the above categories and cannot be included in such a classification.

In those cases in which sufficient data were available, an attempt was made to study the galls on the basis of KÜSTER's division of cecidia into kataplasmas and prosoplasmas. By "kataplasmas" KÜSTER means those indefinite, indeterminate galls whose structure is developed through hyperplasia of embryonic tissue, the end product not becoming in its differentiation, orientation, and form of tissues fundamentally different from the normal plant part. "Prosoplasmas," on the other hand, are highly definite and determinate galls whose structure differs fundamentally from the normal plant, the tissues in their form and orientation characters constituting an aggregation of new qualities. These two groups intergrade, but the intergrading forms are relatively few in number and were classified according to what was believed to be the predominating condition. In all cases where data were not sufficient to pass judgment, the gall was omitted from the census.

Another set of figures presented is that based on KÜSTER's classification of galls into organoid and histoid types. An "organoid" gall is one in which an entire plant organ (leaf, stem,

internode, ovulary, etc.) as a unit suffers modification without a fundamental change in its morphology. The "histoid" galls are those more numerous types in which an entire plant organ is not involved, the gall being more or less definitely appendicular. This group includes all of the prosoplasmas and part of the kataplasmas.

DATA BASED ON NUMBER OF CHAMBERS

Monothalamous galls	408
Polythalamous galls	134
Non-chambered galls	67
Insufficient data to classify	183

The excessively large number of monothalamous forms is a fact related to the character of oviposition. If the eggs are habitually deposited in an aggregate manner, a polythalamous gall is almost certain to result, although there are striking exceptions to this. The great majority of larvae, however, begin their gall-making activity at sufficient distance apart to develop the common monothalamous types of cecidia.

KATAPLASMAS AND PROSOPLASMAS

Kataplasmas	395
Prosoplasmas	322
Insufficient data to classify	73

Viewed from an evolutionary standpoint, the kataplasmas represent the lower levels and the prosoplasmas the higher. That the latter have undergone a considerable expansion indicating relatively rapid progress in recent geologic time is evidenced by the relatively large number of prosoplasmas.

ORGANOID AND HISTOID GALLS

Organoid	215
Histoid	495
Insufficient data to classify	82

These figures have no special significance, perhaps, other than the indication of differences in the range of the gall stimulus. In the organoid types the stimulus is diffused over relatively large areas, inciting all of the tissues of one organ to hypertrophy and hyperplasia. In the histoid forms the stimulus only affects those tissues in a restricted area about the cecidozoon, these tissues responding in a definite and striking manner.

In addition to the above two tables KÜSTER has, in his classification of cecidia, furnished the basis for another table in his analysis of the prosoplasmas. These he divides into four groups: the leaf edge "roll" galls; the diverticulum or outpouching types; the "walled" (umwallungen) forms, whose walls grow up about the superficial larva; and the concentric (mark) cecidia whose larvae inaugurate gall formation from a point within the tissue. In the following list this classification was extended to include so far as possible the kataplasmas also, since a great many of these latter galls can properly be placed under some one of the preceding four groups. The 58 "rosette" and the 28 erineum types cannot be included.

NUMBERS OF VARIOUS GALL TYPES

Leaf edge "roll" types	32	Concentric types	
Diverticulum types		On leaves	145
Leaf or leaflet fold along midvein	19	On stems	184
Pouch types proper	109	On other parts	36
Walled (umwallungen) types	87	Galls unclassifiable in the above categories	86
		Unclassified through insufficient data	94

The factors entering into the production of these various kinds of galls are many; a full discussion of them cannot be presented here. Attention, however, should be called to the two main groups, namely, those which are related to the plant and those related to the cecidozoon. The diverticulum galls are, with few exceptions, only known from the leaf, particularly the blade, since this organ only is sufficiently free from stereome tissues to make possible the characteristic pouching out on the side opposite the cecidozoon. The walled and concentric types can occur on any part of the plant, the latter constituting a much larger aggregation than any of the other kinds. Oviposition within the plant tissue or a migration inward on the part of the larva is necessary for the production of the concentric type of gall. Even in these cases constituting the highest galls, plant factors can exert a modifying influence. The study of the relative importance of the two groups of factors entering into cecidium morphogenesis in specific cases is one of the most valuable and suggestive in the field of zoocecidology.

UNIVERSITY OF ARKANSAS
FAYETTEVILLE, ARK.

LITERATURE CITED

1. CONNOLD, E. T., British vegetable galls. New York. 1902.
2. COOK, M. T., The insect galls of Indiana. 29th Ann. Rept. Dept. Geol. and Natural Hist. Indiana. pp. 801–867. 1904.
3. DARBOUX, and HOUARD, C., Catalog systematique des Zoocécidies de l'Europe at du Bassin méditerranée. Paris. 1901.
4. FELT, E. P., American insect galls. Ottawa Nat. **30**:37–39. 1916.
5. HAIMHOFFEN, G. R., Beobachtungen über die Menge und das Vorkommen der Pflanzengallen und ihre spezielle Verteilung auf die verschiedenen Pflanzengattungen und Arten. Verhandl. Zool.-Bot. Gesell. **8**:285. 1858.
6. HOUARD, C., Les Zoocecidies des Plantes d'Europe et du Bassin de la Meditteranee. 2 vols. Paris. 1909. Vol. 3, Paris. 1913.
7. JARVIS, T. D., A catalog of the gall insects of Ontario. 39th Ann. Rept. Ent. Soc. Ont. 70–98. 1908.
8. KIEFFER, J. J., Synopsis des Zoocecidies d'Europe. Ann. Soc. Entom. France. **70**:233–384. 1901.
9. SCHLECHTENDAL, D. H. R. v., Gallbildungen (Zoocecidien) der deutschen Gefasspflanzen. Zwickau. 1891.
10. STEBBINS, F. A., Insect galls of Springfield, Mass., and vicinity. Bull. 2. Springfield Mus. 1910.
11. THOMPSON, M. T., An illustrated catalog of American insect galls. Edited by E. P. FELT. Nassau, N. Y. 1915.

DIRECT ASSIMILATION OF ORGANIC CARBON BY CERATODON PURPUREUS[1]

WILLIAM J. ROBBINS

(WITH FIVE FIGURES)

Considerable attention has been devoted in recent years to the investigation of the assimilation by green plants of carbon in organic form. Attention has been directed to this phase of plant physiology because of the renewed interest in the relation of the organic compounds found in the organic material of the soil to the growth of green plants, and also because of the light which the result may throw on the question of the products formed in photosynthesis and of the function of various organic compounds in plant metabolism. A number of investigators have shown that higher plants may absorb and assimilate many organic compounds. In 1914 the writer began an investigation of the assimilation of organic compounds by the mosses. Circumstances made it impossible to complete the investigation. The results, however, show some facts and may prove suggestive to those who may continue the work.

SERVETTAZ (**6**) and VON UBISCH (**7**) have made observations upon the assimilation of organic carbon by the mosses. SERVETTAZ grew several species of mosses under sterile conditions on various solid and liquid media. Most of his work was done with *Hypnum purum*. According to SERVETTAZ the mosses when furnished with sugar or some other organic substance are able to live in the dark and become green slowly; but under these conditions they do not form starch and their increase is never important. Levulose, lactose, maltose, and saccharose when present at a concentration of 5 parts per 1000 favor development, but 2 parts per 100 are decidedly toxic. Dextrine, starch, and gum arabic at a concentration of 5 parts per 1000 retard development, but at 2 parts per 1000 favor it. *Hypnum purum* prefers the

[1] Published by permission of the Director of the Alabama Agricultural Experiment Station.

hexoses. Grown in the light in a mineral solution containing sugar, SERVETTAZ found that in 4 months *Hypnum purum* assimilated sugar, as given in table I.

TABLE I

Sugar	Original amount of sugar	Sugar used
Glucose	0.25 gm.	0.07 gm.
Levulose	0.25	0.065
Lactose	0.25	0.01
Maltose	0.25	0.005
Cane sugar	0.25	0.012

SERVETTAZ also found that peptone is assimilated by the mosses if present in concentrations below 2 parts per 1000. Inulin apparently is not assimilated.

The observations by VON UBISCH on the assimilation of organic carbon by the mosses were few. He grew several species of mosses in pure culture and noted the presence of large starch grains in the protonema of *Funaria hygrometrica* grown in the dark on a nutrient agar containing peptone and glucose. On the same agar lacking peptone and glucose the starch grains were very small.

Investigation

Although SERVETTAZ and VON UBISCH both obtained pure cultures from the spores in the capsules of various mosses, the moss used in this work was accidentally obtained in pure culture. It was found growing as a contamination in one of the culture vessels used by KNUDSON (3) in his investigation of the assimilation of organic compounds by the higher plants. Transferred to a nutrient agar it grew well. The protonema penetrated the soft agar and moss plants eventually were produced. It was identified as *Ceratodon purpureus* L. by Dr. A. L. ANDREWS of Cornell University, to whom the writer expresses his thanks.

USE OF ORGANIC CARBON.—Preliminary experiments showed that *Ceratodon purpureus* can assimilate organic carbon. In test tubes on a nutrient agar containing glucose the growth in the light was 4 or 5 times as luxuriant as on the nutrient agar lacking

glucose. The heavy dark green mat formed on the glucose agar is shown in fig. 1. This photograph was made 1 month after inoculation.

In solution cultures the utilization of the glucose was shown even more clearly. Fifty cc. of Czapek's nutrient solution for fungi (2) plus 0.1 gm. of calcium chloride per liter was placed in 125 cc. Erlenmeyer flasks. To some of the flasks 3 per cent glucose was added. All were sterilized and inoculated with the

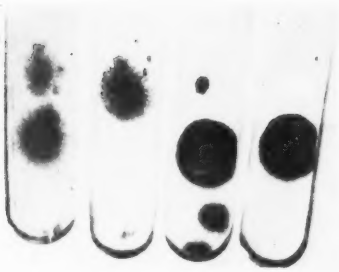


FIG. 1

FIG. 2

FIGS. 1, 2.—Fig. 1, *Ceratodon purpureus* grown 1 month in light on nutrient agar: 2 tubes to left contain no glucose; 2 tubes to right contain glucose; fig. 2, *Ceratodon purpureus* grown in dark for 1 month in modified Czapek's solution: flask to left contains 3 per cent glucose; flask to right contains no organic compound.

moss by transferring a bit of the protonema growing on agar in a test tube. Some of the flasks were placed in a north window and others in a dark cupboard. At the end of a month and a half it was found that in the light far more growth had occurred in the flasks containing glucose. In the glucose solution only protonema had developed; in the check young moss plants had been formed. In the dark no growth had occurred in the check, while the solutions in those flasks containing glucose were completely filled with a mass of dark reddish brown colored protonema (fig. 2).

AVAILABILITY OF DIFFERENT FORMS OF CARBON.—The culture solution used was one devised by MOORE for the culture of algae,

and is described by REED (5). The carbon compounds were all Merck's products. Dextrose, pure, "Mulford" and Schering's levulose were also used in repeating some of the experiments.

Sufficient of the organic compound was added to make a concentration of 0.1 mol. The culture vessels were 125 cc. Erlenmeyer flasks, containing 50 cc. of solution. Those sugars, such as cane sugar, which could be hydrolyzed were sterilized in an Arnold sterilizer and tested for hydrolysis before use. After sterilization

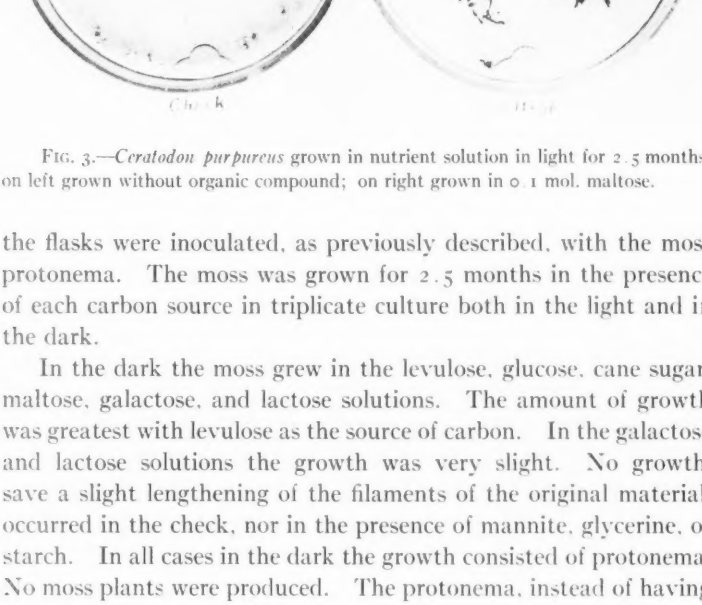


FIG. 3.—*Ceratodon purpureus* grown in nutrient solution in light for 2.5 months: on left grown without organic compound; on right grown in 0.1 mol. maltose.

the flasks were inoculated, as previously described, with the moss protonema. The moss was grown for 2.5 months in the presence of each carbon source in triplicate culture both in the light and in the dark.

In the dark the moss grew in the levulose, glucose, cane sugar, maltose, galactose, and lactose solutions. The amount of growth was greatest with levulose as the source of carbon. In the galactose and lactose solutions the growth was very slight. No growth, save a slight lengthening of the filaments of the original material, occurred in the check, nor in the presence of mannite, glycerine, or starch. In all cases in the dark the growth consisted of protonema. No moss plants were produced. The protonema, instead of having

the familiar yellow color of chlorotic higher plants, was a dark reddish brown.

By the use of iodine starch was demonstrated in the protonema grown in the levulose, glucose, cane sugar, maltose, galactose, and lactose solutions. The protonema grown in the levulose solution contained the most starch. At the end of the experiment it was found that the cane sugar was completely inverted. The use of Barfoed's solution and the osazone test failed to demonstrate the

FIG. 4.—*Ceratodon purpureus* grown in nutrient solution in light for 2.5 months: on left grown in 0.1 mol. dextrose; on right in 0.1 mol. levulose.

presence of glucose in the maltose solution. No glucose was found in the lactose solution.

In the light there was growth in all the cultures, showing that none was toxic to the moss. The greatest amount of growth was found in the levulose solution. Moss plants developed in all cultures. To some extent the macroscopic appearance of the growth in the light seemed to be influenced by the particular sugar used. For example, in the glucose solution sharp clean cut moss plants were produced. In the levulose solution many moss plants were formed, but they were shorter and thicker. This difference in the moss plants and the excess of protonema in the levulose solution gave the culture as a whole a woolly appearance. The

effects of glucose, levulose, and maltose on the moss are shown in figs. 3 and 4. The cultures also differed in color. The protonema in the levulose, glucose, and cane sugar was brownish at the end of the experiment; while in the lactose, maltose, and check it was still a normal green.

COMPARISON OF LEVULOSE AND GLUCOSE AS CARBON SOURCES.—In the preceding experiment the growth when levulose was the source of carbon was so much greater in amount (fig. 5) than that when glucose was the source of carbon that a further comparison of the effects of the two sugars was made. The moss was grown from

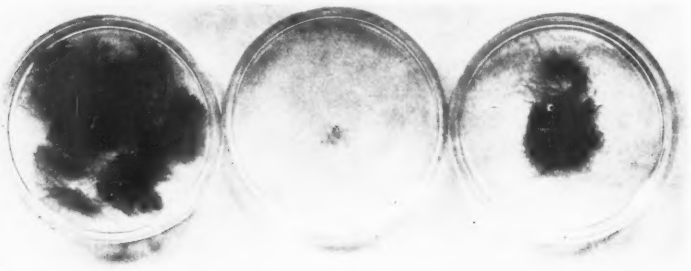


FIG. 5.—*Ceratodon purpureus* grown in dark for 2 months in nutrient solution: from left to right, 0.1 mol. levulose, no carbohydrate, 0.1 mol. glucose.

November 27 to February 24 in the modified Czapek's solution mentioned. Triplicate cultures were grown in the light and in the dark. The dry weight of the moss was determined by filtering the protonema and moss plants into a Gooch crucible and drying at 110° C. The sugar determinations were made by the use of Fehling's solution. The results are given in table II and represent the averages of the data for triplicate cultures.

The sugar analyses given in table II show an unmistakable consumption of sugar in all cases. More levulose was used than glucose. In the case of levulose the greater consumption of sugar occurred in the dark. In the case of glucose the greater consumption occurred in the light. Comparing the dry weights of the moss protonema and plants in the check, glucose, and levulose solutions, it is evident that the sugar has greatly increased the

amount of dry matter. The dry matter of the moss grown in the solution containing levulose is much greater than that of the moss grown in the solution containing glucose. In the light twice as much dry matter was formed with levulose as the carbon source than with glucose as the source of carbon. In the dark there was produced in the levulose solution 7 times as much dry matter as was formed in the glucose solution.

TABLE II

Solution	Average dry weight of moss	Original sugar per 50 cc.	Sugar used per 50 cc.	Sugar over dry weight
	gm.	gm.	gm.	
Levulose in light	0.0634	0.7700	0.1100	1.7
Levulose in dark	0.0854	0.7700	0.1650	1.9
Glucose in light	0.0345	0.8970	0.0440	1.3
Glucose in dark	0.0115	0.8970	0.0360	3.1
Check, no organic carbon in light	0.0074	.....	.....	.....
Check, no organic carbon in dark	Inappreciable	.....	.....	.....

Discussion

It is evident that the moss used in these experiments can absorb and utilize organic carbon. The experiments do not demonstrate that the mosses under field conditions, in competition with both the bacteria and the fungi, benefit from the organic compounds in the soil. They do suggest, however, that if suitable organic compounds are present in the soil solution they will be absorbed and used by the moss with advantage.

The results at present seem to bear little on the problems of the products formed in photosynthesis. It is an interesting fact, however, that starch was formed from the maltose and lactose, although no evidence was found that either of these sugars was hydrolyzed. They may have been hydrolyzed within the moss cells, or the products of hydrolysis may have been assimilated as fast as they were formed. In either of these cases evidence of the hydrolysis would have escaped the methods used in looking for it. It should also be noted that the growth in the lactose solution was very slight. An examination of the moss for the enzymes, maltase and lactase, would seem pertinent.

The differences in the growth in the levulose and glucose solutions are of considerable interest. BROWN and MORRIS (1), working with *Tropaeolum majus*, believe that glucose is more quickly used up for respiration and possibly also for tissue forming than is levulose. LINDET (4), working with the yeast and fungi, concluded that glucose is mainly concerned in respiration, while levulose is more particularly concerned in the elaboration of tissue. In the case of *Ceratodon purpureus* the elaboration of tissue is certainly far greater with levulose than with glucose. The data, although not conclusive, also suggest that the elaboration of tissue in the presence of levulose is more economical than in the presence of glucose, as the sugar used per unit of dry matter formed is generally smaller in the levulose than in the glucose solution.

Summary

1. Under the conditions of the experiments reported organic carbon in the form of levulose, glucose, galactose, lactose, cane sugar, and maltose is absorbed and utilized by *Ceratodon purpureus*.

2. Starch is formed in the dark from levulose, glucose, galactose, lactose, cane sugar, and maltose.

3. Mannite, glycerine, and starch cannot be utilized by this moss.

4. The amount of growth with levulose as the source of carbon is 2–7 times greater than that with glucose as the source of carbon.

5. In the presence of levulose the greater amount of growth occurs in the dark. With glucose the greater amount of growth occurs in the light.

6. Light seems to be necessary for the formation of moss plants, even though available carbohydrate is furnished.

ALABAMA POLYTECHNIC INSTITUTE
AUBURN, ALA.

LITERATURE CITED

1. BROWN, H. T., and MORRIS, G. H., A contribution to the chemistry and physiology of foliage leaves. Jour. Chem. Soc. Trans. **63**:604–677. 1893.
2. DOX, A. W., The intracellular enzymes of *Penicillium* and *Aspergillus* with special reference to those of *Penicillium camembertii*. U.S. Dept. Agric., Bur. An. Ind. Bull. 120. pp. 70. 1910.

3. KNUDSON, L., Influence of certain carbohydrates on green plants. Cornell Univ. Agric. Exp. Sta. Mem. **9**:1–75. *figs. 11.* 1916.
4. LINDET, L., Sur le pouvoir électif des cellules végétales vis à vis du dextrose et du lévulose. Compt. Rend. **152**:775–777. 1911.
5. REED, H. S., The value of certain nutritive elements to the plant cell. Ann. Botany **21**:501–543. *figs. 2.* 1907.
6. SERVETTAZ, CAMILLE, Recherches experimentelles sur le développement et la nutrition des mousses en milieux stérilisés. Ann. Sci. Nat. Bot. IX. **17**:111–224. *pls. 4. figs. 11.* 1913.
7. VON UBISCH, G., Sterile Mooskulturen. Ber. Deutsch. Bot. Gesells. **31**:543–552. *figs. 10.* 1913.

SYSTEMATIC RELATIONSHIP OF CLITHRIS

LEO R. TEHON

(WITH PLATE IX)

The genus *Clithris* was described by FRIES (Syst. Myc. **2**:186) in 1823. Apparently unaware of this earlier description, WALLROTH (Crypt. **2**:422) erected the genus *Colpoma* in 1833, and CORDA (Icon. **5**:34) the genus *Sporomega* in 1840. FRIES'S genus was entirely overlooked and the two others accepted, so that they appear in SACCARDO'S *Sylloge Fungorum* (**2**:801; **5**:1127) in 1883 and 1891. In 1896, however, REHM (Rabenh. Krypt. Fl. **3**:101) called attention to the earlier name as follows:

> Unter obigem Namen (*Clithris* 1823), welcher die Priorität besitzt, stelle ich sowohl *Colpoma* Wallr. 1833! mit aussen bereiften Apothecien, als *Sporomega* Corda 1840! mit schwarzen Apothecien zusammen, da der innere Bau, wie die Entwicklungsweise der Apothecien bei beiden die gleichen sind.

In his subsequent treatment of the genus *Clithris*, nearly all of the species are listed which were included by SACCARDO under *Colpoma* and *Sporomega*. SACCARDO (Sylloge Fung. **18**:165) in 1906 accepts REHM'S correction and records *Colpoma* and *Sporomega* as synonyms of *Clithris*.

FRIES and KARSTEN (Mycol. Fenn. **1**:221) placed *Clithris* next to *Cenangium*, while QUÉTLET (Enchir. Fung. 330) placed *Colpoma* among the Patellariaceae. SACCARDO at first listed *Colpoma* and *Sporomega* with the Hysteriales; but later, combining the two genera under *Clithris*, he places the whole with the Phacidiales.

In the light of what has just been said, the taxonomic relationship of the genus may appear uncertain; and, indeed, when specimens are examined, the difficulty is seen to be real. Characterized by a more or less linear ascoma which opens by a longitudinal split, the superficial aspect fits very well into the concept of an Hysteriaceous form. When there is added to this the fact that in many specimens the split is small and does not expose very widely the fruiting disk, the Hysteriaceous aspect is strengthened. It is not

surprising, therefore, that the position of *Clithris* has been questioned. That these superficial characters are not sufficient for a full diagnosis of relationship becomes at once evident, and the need of an exact statement is obvious.

In making the present study, there have been available authentic specimens of *Clithris quercina* (Pers.) Rehm (Fungi Selecti Exsiccati, *Roumeguére*, no. 268, and Mycotheca Universalis, *De Thumen*, no. 369); *C. verrucosum* Wallr. (Fungi Selecti Exsiccati, *Roumeguére*, no. 2827); *C. andromedae* (Schwein) Lindau (North American Fungi, *Ellis*, no. 155); and, through the kindness of E. A. BURT of the Missouri Botanical Gardens, *C. crispa* (Pers.) Rehm (*Romell*, Fungi Exsiccati Praesertim Scandinavici, no. 85). In addition to these, use has been made of the new species described in this paper.

Material from all of these specimens has been sectioned and studied, and camera lucida drawings made of such as are not already illustrated. An examination of sectioned and unsectioned ascomata showed the following:

1. The fruiting disk is large and of densely crowded asci and paraphyses (figs. 3, 6, 8–11). This is a thoroughly Phacidiaceous character, distinct from Hysteriaceous forms, where the fruiting disk is small and seldom with asci and paraphyses overcrowded.

2. The ascigerous hymenium is characteristically Discomycetous in nature (figs. 3, 6, 8–11). The Hysteriales are regarded as forming a bridge between the Discomycetes and the Pyrenomycetes; and consequently the more disklike the hymenium the less relationship the form may be expected to bear toward the Hysteriales.

3. The opening of the ascoma is a true split (figs. 8–10). Its edges are jagged and torn; it is wider at some places than at others; and portions of the edges are frequently broken completely away in the tearing (figs. 2, 11). Opposed to this character is the rather regular appearance of the edges of the openings in Hysteriaceous forms which suggests that the slit there is an elongated ostiole rather than a true split or tear.

4. The tendency in the specimens examined is to find the fruiting disk in places rather widely exposed, either by the wide bending back of the sides of the ascoma (figs. 3, 10) or by the

breaking off of portions of the top (figs. 6, 11). Hysteriaceous forms have the fruiting disk nearly or quite covered.

Strengthening these observations are the conditions to be observed in the new species of *Clithris* herewith described. *C. clusiae* (figs. 2, 3) shows the characteristically Discomycetous hymenium, and the tendency to expose the fruiting disk by the breaking off of portions of the roof of the ascoma. In the section it will be seen that the top has broken away completely, thus leaving the entire fruiting disk exposed. Almost the same conditions are to be found in *C. minor*. *C. pandani* (fig. 6) likewise shows the characteristically Discomycetous hymenium. Of the top of the ascoma there remain only small projections on either side. The center has broken away, leaving a very large part of the fruiting disk exposed.

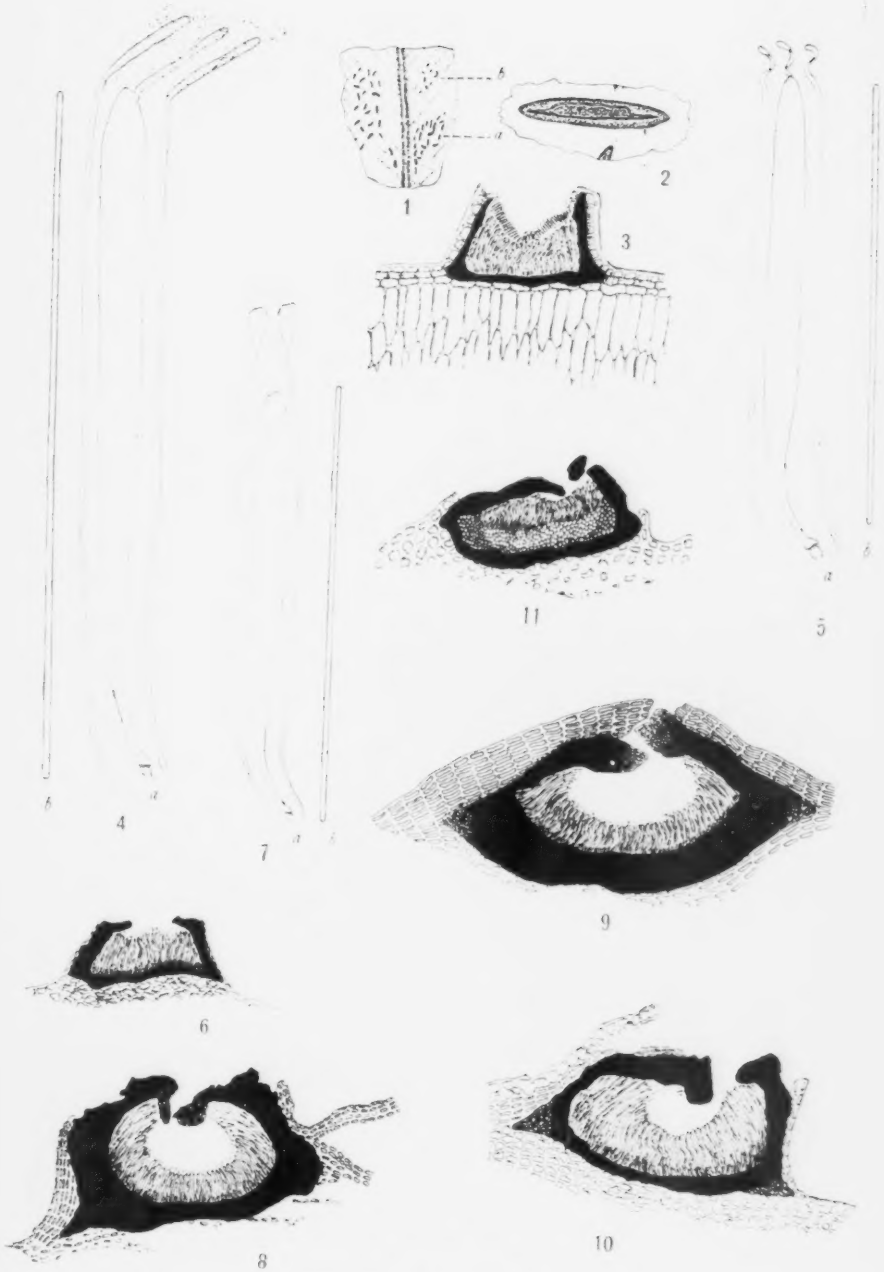
CLITHRIS Fries, 1823.—As originally described, *Clithris* is characterized in part by the possession of paraphyses coiled at the tip. Obviously, the form of the tips of the paraphyses cannot be held as a generic character, since the three species here described, which are clearly congeneric, show certain variations as regards the paraphyses tips, one only possessing the characteristic coiling. These species were collected by F. L. STEVENS in Porto Rico, and it is through his kindness that the author is allowed to include descriptions of them in this paper.

Clithris clusiae, sp. nov.—Spots 0.5–2 cm. in diameter, pale to yellow, uniformly dotted with the ascomata. Ascomata dark, subepidermal, erumpent, 950×468 μ, rupturing with the epidermis in a long slit. Paraphyses filiform, numerous, coalescing above in a pale yellow epithecium. Asci long, narrow, 150×7–8 μ, 8-spored; spores filiform, 1×150 μ, fragmenting when mature, pale smoky or light brown.

On dead leaves of *Clusia rosea*. Desecheo Island no. 1595 (type).

The ascomata of this species are to be found not only in spots on the leaf blade but also clustered very thickly on the petiole and the midrib. The paraphyses are not coiled apically, but slightly enlarged and straight. The tip bends just above the top of the asci, as is shown in fig. 4*a*.

Clithris minor, sp. nov.—Spots similar to those of *C. clusiae*. Ascomata small, dark, 624×220 μ. Paraphyses numerous, filiform,



TEHON on CLITHRIS

hyaline, slightly exceeding the asci and coiled apically to form a thin, hyaline epithecium. Asci long, narrow, 110×7 μ, 8-spored; spores filiform, 1×110 μ, fragmenting when mature, and pale smoky in color.

On dead leaves of *Clusia rosea*. Desecheo Island, no. 1595 (type).

Although occurring on the same leaf with *C. clusiae*, *C. minor* is readily distinguished by its smaller size, and by the abundance of hyaline paraphyses which only slightly exceed the asci and are coiled apically, forming a thin, hyaline epithecium.

Clithris pandani, sp. nov.—Spots 0.25–1 cm. in diameter, otherwise similar to those of *C. clusiae* and *C. minor*. Ascomata small, dark, subepidermal, erumpent, 570×110 μ. Paraphyses numerous, exceeding the asci and united above into a pale yellowish epithecium. Asci long, narrow, 91×7 μ, 8-spored; spores filiform, 1×91 μ, fragmenting when mature, and pale smoky in color.

On dead leaves of a cultivated species of *Pandanus*. San Juan, no. 4090 (type).

This species is the smallest of the three; otherwise its superficial characteristics are much like those of *C. clusiae* and *C. minor*. The tips of the paraphyses are expanded above (but not coiled) and united into a pale yellowish epithecium.

Types of these species are deposited in the Herbarium of the University of Illinois.

University of Illinois

EXPLANATION OF PLATE IX

Fig. 1.—Habitat sketch: *a*, *C. clusiae*; *b*, *C. minor*.
Fig. 2.—Habitat sketch of *C. clusiae*, enlarged.
Fig. 3.—*C. clusiae*: section of ascoma.
Fig. 4.—*C. clusiae*: *a*, asci and paraphyses; *b*, spore.
Fig. 5.—*C. minor*: *a*, asci and paraphyses; *b*, spore.
Fig. 6.—*C. pandani*: section of ascoma.
Fig. 7.—*C. pandani*: *a*, asci and paraphyses; *b*, spores.
Fig. 8.—*C. crispa*: section of ascoma.
Fig. 9.—*C. andromedae*: section of ascoma.
Fig. 10.—*C. quercina*: section of ascoma.
Fig. 11.—*C. verrucosum*: section of ascoma.

STRUCTURE OF WOOD IN BLUEBERRY AND HUCKLEBERRY[1]

ESTHER MARGARET FLINT

(WITH PLATES X, XI)

According to EAMES,[2] the anatomy of the northern oaks is characterized by small uniseriate rays, and large ones which are many cells in width and generally fusiform in shape. It has been shown in this article that the large rays have developed from the aggregation of small ones through the transformation of fibers into parenchyma. As evidence he figures the wood of *Quercus*, especially seedlings, to elucidate the broad ray in the process of formation by fusion of small rays, and the gradual transformation of the separating fibers into parenchymatous elements. A study of the material investigated by EAMES justifies his conclusion. As a preliminary to the present investigation, some illustrations of the anatomy of a seedling oak have been introduced. Fig. 1 shows in tangential view a portion of the wood of the epicotyl of *Quercus velutina* with two characteristic kinds of rays. The broad ray in the central part is plainly in the process of formation, the parenchyma cells being interspersed with fibers in all stages of division and transformation into parenchyma. Fig. 2 is a transverse view of the situation in fig. 1. The broad ray here shows two kinds of cells, the dark parenchymatous ones, and the lighter ones which represent more or less modified fibers. Fig. 3 shows a view in the same plane as fig. 1, but more highly magnified. The manner in which the ray becomes solidly parenchymatous is even more apparent here, especially at the left of the figure, where we see a fiber partially divided into parenchyma cells.

With this preliminary reference to the anatomy of *Quercus*, it is possible to pass advantageously to the consideration of the anatomy of *Vaccinium* and allied genera, which show interesting and strik-

[1] Contribution from the Laboratory of Plant Morphology of Harvard University.

[2] EAMES, A. J., On the origin of the broad ray in *Quercus*. BOT. GAZ. **49**:161–167. *pls. 8, 9.* 1910.

ing points of similarity with the conditions already mentioned. *V. corymbosum*, as shown in transverse view by fig. 4, is seen to have broad and also uniseriate rays, as does *Quercus*. Although the large rays are not so broad as the corresponding rays of the oak, yet they are similar to the latter in the strong contrast which they present to the small uniseriate ones. The large ray of *V. corymbosum* (fig. 4) is composed of two kinds of cells: light, rather larger ones; and dark, smaller ones (the ordinary parenchymatous ray cells), a condition which exactly parallels the organization of the ray of the oak just noted. Fig. 5 shows a portion of this same transverse view of the wood of the stem of *V. corymbosum* more highly magnified, so that the twofold composition of the ray becomes even more apparent. Fig. 6 is a tangential aspect of the wood of the stem of *V. corymbosum* corresponding to fig. 4. In this plane also the two kinds of rays, uniseriate and broad, are likewise visible. The presence of two kinds of cells in the large ray, one dark and rather small, the other light and somewhat larger, can also be distinguished clearly. Obviously the large ray is a compound structure, just as has been proved in the case of the corresponding large rays of the oak, with which the large ray of *V. corymbosum* appears to be identical in so far as it is composed of the two kinds of cells described.

Vaccinium pennsylvanicum shows the same situation as *V. corymbosum*, as is vouched for by figs. 7 and 8. In fig. 7 the contrast between broad and narrow rays is readily distinguished. The large number of light colored cells present in the broad ray plainly shows indication of origin from the transformation of fibrous elements into parenchyma. An enlarged view of this situation is given in fig. 8, which represents a higher magnification. The light cells are strikingly different from the ordinary ray cells which they accompany, and the seriate ones in the central portion are obviously derived from a transformed fiber. The whole structure is consequently a compound ray resembling that found in the wood of the oak. In fig. 9 the same condition is noted as in fig. 7, namely, rays of two sharply contrasting types, broad and uniseriate. Of these the large ones are compound in structure, showing derivation by the fusion of small rays as well as by the transformation

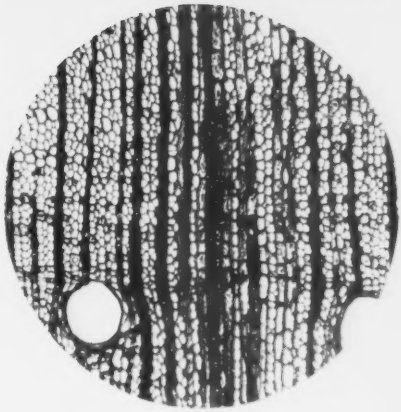
of fibers into parenchyma cells. This figure represents in tangential view the wood of the root of *Gaylussacia*, a genus closely allied to *Vaccinium* and having identical ray structure, as is seen by the comparison of the two woods illustrated in figs. 7 and 9.

Fig. 10 is a tangential view of the wood of the root of *Rhododendron*, a genus also allied to *Vaccinium* although not so closely as is *Gaylussacia*. The wood as shown here is much like that of the northern oaks, especially in the marked contrast between its large and small rays. The construction of the ray itself in *Rhododendron*, however, is more clearly seen in fig. 11, a transverse section of the same wood. The interspersion of the light colored fibrous elements through the ray at once shows its composite character, and although it does not illustrate actual transformation of fibers into radial parenchyma, it points the way to that as a natural solution of the origin of the broad ray in this genus.

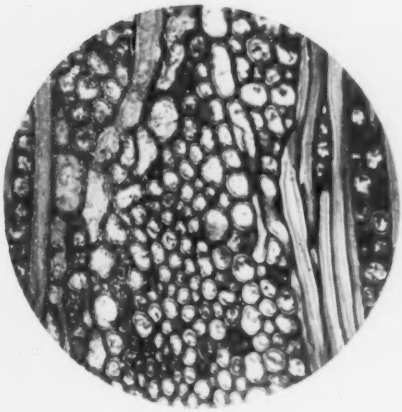
In regard to *Vaccinium* and the allied *Gaylussacia* it is now clear that the large rays in these genera are of the same nature as those of *Quercus*, and like them are in strong contrast to the more numerous uniseriate rays. In *Rhododendron* also we noted the same condition, albeit its origin was not in all respects so clear. That this condition of *Vaccinium* and allied genera, which is so similar to that found in the oak, is not common to all ericaceous woody types, is evidenced by fig. 12, which shows in tangential view the wood of the stem of a species of *Arbutus*. The rays of this wood do not fall into two strongly contrasting categories, the broad and the uniseriate. Rather do they grade into each other and are only relatively broad or narrow when compared with each other. In this respect *Arbutus* presents the general situation for forest trees, the majority of which do not possess contrasted broad rays and uniseriate rays, but have all their rays comparatively small and of intergrading dimensions.

From this examination of the genus *Vaccinium* and other genera allied to it, and the comparison of them with the wood of *Quercus*, we must conclude that the well known large rays of the latter have their counterparts in the somewhat smaller rays of *Vaccinium* and *Gaylussacia*. These rays, although of considerably smaller dimensions, are in just as marked contrast to the accompanying

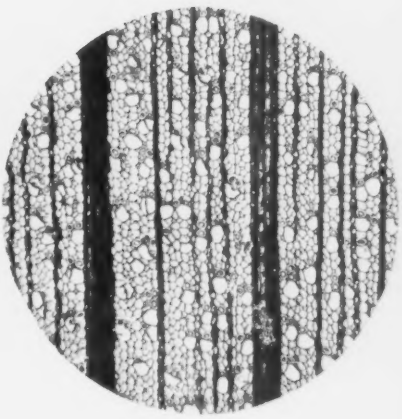
1



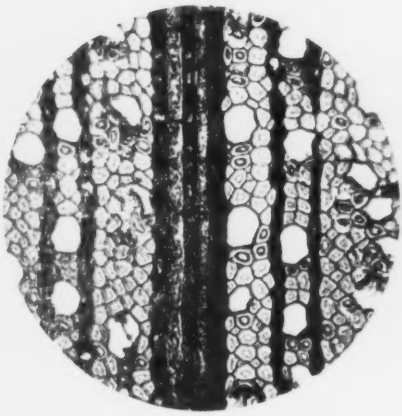
2



3



4



5

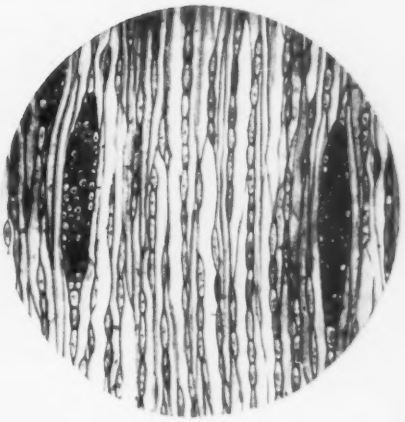
6

FLINT on VACCINIUM

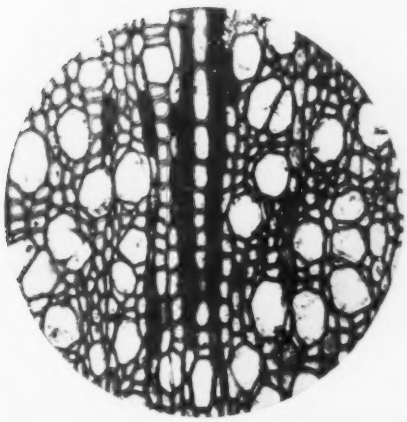
7

8

9



10



11

12

FLINT on VACCINIUM

uniseriate rays as are the broad rays in *Quercus*. Because of this sharp contrast, and because of the similar origin of the broad rays, they are obviously the exact counterparts of the broad parenchymatous bands in the secondary wood of *Quercus*.

In conclusion, I wish to thank Dr. E. C. JEFFREY of this laboratory for material and advice rendered during the course of this investigation.

HARVARD UNIVERSITY
CAMBRIDGE, MASS.

EXPLANATION OF PLATES X, XI

FIG. 1.—Longitudinal tangential section, aggregate ray of seedling of *Quercus velutina;* ×100.

FIG. 2.—Transverse section, wood of seedling of *Q. velutina;* ×100.

FIG. 3.—Longitudinal tangential section, wood of *Q. velutina;* ×200.

FIG. 4.—Transverse section, wood of stem of *Vaccinium corymbosum;* ×100.

FIG. 5.—Transverse section, wood of stem of *V. corymbosum;* ×200.

FIG. 6.—Longitudinal tangential section, wood of stem of *V. corymbosum;* ×100.

FIG. 7.—Longitudinal tangential section, wood of subterranean stem of *V. pennsylvanicum;* ×100.

FIG. 8.—Longitudinal tangential section, wood of root of *V. pennsylvanicum;* ×200.

FIG. 9.—Longitudinal tangential section, wood of root of *Gaylussacia* species; ×100.

FIG. 10.—Longitudinal tangential section, wood of root of *Rhododendron* species; ×100.

FIG. 11.—Transverse section, wood of root of *Rhododendron* species; ×200.

FIG. 12.—Longitudinal tangential section, wood of stem of *Arbutus* species; ×100.

BRIEFER ARTICLES

PURPLE BUD SPORT ON PALE FLOWERED LILAC (SYRINGA PERSICA)

(WITH ONE FIGURE)

In the present state of our knowledge of bud sports, every well authenticated case is distinctly worthy of record. Fig. 1 represents a panicle of a bud sport of the Persian lilac, and beside it a panicle of the form on which it appeared. The bush is one of the very pale-flowered varieties, by no means white, which is best described as lilac-tinged. The bud sport was deep purple, of exactly the same color as the darkest flowered variety of the Persian lilac commonly grown. The sport was free from all suspicion of being a graft, occurring, as it did, at the summit of a bush 10 ft. high, which had never been grafted, with normal panicles of the same age below it. The bush has flowered for 10 years or more, without ever having produced any other than tinged flowers. Dr. LOUIS P. HALL, of Ann Arbor, on whose grounds it occurred, and who called it to our attention, is a keen observer, and would surely have noticed unusual panicles if there had been any before this year. Particular pains were taken to ascertain that the sport was truly such, and not a graft, for grafted lilacs are, of course, not uncommon. The evidence that the dark-colored inflorescence was the result of a bud sport was altogether clear.

The flowers of the variation differed from those of the form on which it occurred not only in color but also in size. Data for several size characters, based in each case upon 50 measurements, are as follows:

	Normal form	Purple bud sport
Spread of corolla		
Range	10.4–13.3 mm.	15.3–18.4 mm.
Mean	12.2	16.6
Length of tube		
Range	9.0–11.9	10.2–11.8
Mean	11.3	11.1
Width of corolla lobes		
Range	2.7–4.1	4.0–5.5
Mean	3.6	4.75

It is evident that the chief size differences are in the spread of the corolla and the width of its lobes. The ranges of variation for these characters hardly overlap in the two forms.

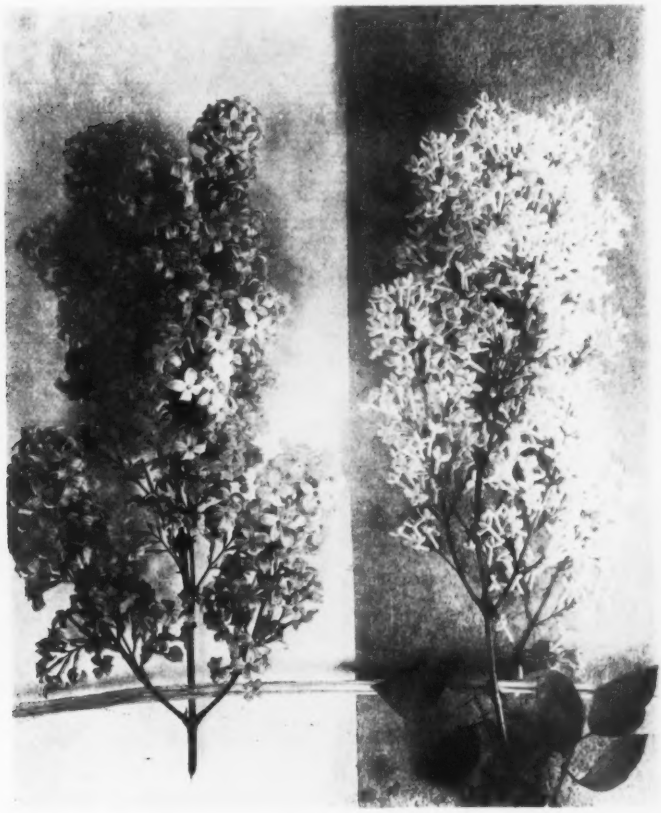


FIG. 1.—*Syringa persica:* at left, large-flowered purple bud sport; at right, normal inflorescence of small-flowered, lilac-tinged variety.

In both measurements and color, the bud sport exactly duplicated a dark purple variety of *Syringa persica* which is commonly cultivated. The latter differs from the lilac-tinged variety in that the corolla-lobes appear to be 3-nerved rather than 1-nerved. In this character, also, the bud sport was different from the bush that produced it, and exactly

like the purple variety. Microscopic examination showed that what appeared to be lateral nerves were not due to bundles, but were merely folds. Nevertheless they afford a striking character difference between the two forms.

The bushes under consideration are identified as *Syringa persica* with some doubt. The upper surface of the leaves lacks stomata, which should be present in *S. persica*, as defined by SCHNEIDER in his *Handbuch der Laubholzkunde*. The flowers are sterile, a fact which would presumably point to a hybrid ancestry, and the terminal bud is not suppressed, but generally gives rise to a panicle. The flowers are produced, then, from lateral and terminal buds on the wood of the preceding year. The bushes were purchased as *S. persica*, which seems, on the whole, the most applicable name.

The color of the wild lilacs is purple. A light-colored variety, such as the one which produced this bud sport, might be judged, a priori, to be a Mendelian recessive. If it should be found to be so, the reversion to the original purple would be distinctly interesting, from the standpoint of the now almost discarded presence and absence hypothesis. If not a reversion, it might be either a case of what has been called somatic segregation, or a periclinal chimaera. These hypotheses will be tested, if possible; but since the evidence, if obtainable at all, must be long delayed, it is thought worth while to report the mere fact that such a bud sport has been observed.—FRIEDA COBB AND H. H. BARTLETT, *University of Michigan, Ann Arbor, Mich.*

METHOD FOR STAINING ANTHEROZOID OF FERN

(WITH ONE FIGURE)

Some time ago the writer had a favorable opportunity to study spermatogenesis in some of the common ferns, and it was found desirable to perfect a staining technique by means of which it was possible to stain the cilia and at the same time to differentiate clearly the different parts of the body of the antherozoid. Of the various methods employed the following proved most satisfactory: (1) kill antherozoids in a drop of water on a slide by inverting the slide over a vial containing a 1 per cent osmic acid solution (the drop of water should be small and when placed on the slide spread out so as to form a thin film); (2) dry slide in air; (3) stain in safranin 10 minutes to 1 hour; (4) wash in water; (5) wash in 95 per cent alcohol until only the nucleus remains stained; if necessary,

use xylol to clear and then remove the xylol with 95 per cent and absolute alcohol; (6) stain in acid fuchsin 10–20 seconds; (7) wash in absolute alcohol; (8) clear in clove oil and xylol; (9) seal in balsam.

The nucleus is stained a bright red by the safranin, while the cytoplasmic portions of the antherozoid are stained a bluish pink. The blepharoplast is more densely stained than the cytoplasmic envelope.

FIG. 1.—Antherozoid of *Onoclea struthiopteris*; ×3700 and reduced one-half in reproduction.

The cilia of the antherozoid are attached for some length along the blepharoplast, as shown in fig. 1. No cilia are attached to the extreme anterior portion of the blepharoplast. The envelope at the anterior end extends a short distance beyond the nucleus, which is small and rodlike at this extremity. The nature of the denser portions in the envelope is not understood. These were of constant occurrence when the method described was used. They could also be readily observed in the living antherozoid. Some very good results were obtained when iron haematoxylin was substituted for the safranin.—W. N. STEIL, *University of Wisconsin, Madison, Wis.*

CURRENT LITERATURE

BOOK REVIEWS

Botany of crop plants

A notable impetus to the study of botany in agricultural colleges and to the study of agricultural plants and problems in botanical departments generally is bound to be given by ROBBINS' recent volume on the botany of crop plants.[1] About 70 pages are devoted to a brief summation of some of the more important topics in general botany, under the headings: the seed plant body, fundamental internal structures, roots, stems, leaves, flowers, fruits, seeds and seedlings, and the classification and naming of plants. The body of the book presents in compact and pleasing form the botanical features of our chief crop plants, arranged in the familiar taxonomic sequence from grasses to composites. For each crop there is a discussion of the chief botanical features relating to habit, structure, and behavior, a classification (often with a key), a consideration of the chief uses, and a list of the more important references. As a sample of the mode of treatment we may take corn, to which 35 pages are devoted. The paragraph headings under corn are habit of plant and roots, prop roots, stem, leaves, inflorescence, staminate inflorescence, staminate spikelet, pistillate inflorescence, pistillate spikelet, hermaphroditic flowers, opening of the flowers and pollination, fertilization and development of the grain, xenia, variation, results of self-fertilization, the mature grain, corn starch, germination, classification, origin, environmental relations, uses, production, and references.

The compactness and up-to-dateness of the information in this book are among its most commendable features. It is doubtful if there is any other place where one may find so quickly and satisfactorily botanical information about our common crops. While the volume was written primarily as a textbook for botanical courses in agricultural colleges, a field which was far from adequately filled, this book should be on the shelf of every botanical teacher and investigator, because of its value as a source of ready and reliable information. The publishers also may be commended for the neat and pleasing appearance which the book presents.—H. C. COWLES.

MINOR NOTICES

Flora of Bermuda.—BRITTON[2] has published an illustrated *Flora of Bermuda* which is attractive in appearance and unusually inclusive in its contents. The land area is a little over 19 square miles, or about one-fourth the size of

[1] ROBBINS, W. W., The botany of crop plants. pp. xix+681. *figs. 263.* Blakiston's Son & Co. Philadelphia. 1917.

[2] BRITTON, NATHANIEL LORD, Flora of Bermuda. 8vo. xi+585. *figs. 519.* New York: Scribner's Sons. 1918. $4.50.

Staten Island, but the flora calls for a book of nearly 600 pages. About 80 per cent of the land plants occur also in the West Indies or southern Florida or both, while about 8.7 per cent of the total native flora is endemic, "there being 61 species in Bermuda or its waters not known to grow naturally anywhere else in the world." The representation of groups by the native species is as follows: Spermatophytes 146, Pteridophytes 19, Bryophytes 51, Lichens 80, Fungi 175 (at least), Algae 238, making a total of 709 species. The volume contains descriptions and illustrations of 519 species of Spermatophytes, Pteridophytes, and Bryophytes, and also accounts, not illustrated, of the Lichens, Fungi, and Algae.

The excellent text cuts, simple keys, and clear descriptions should make the volume a very effective introduction to an interesting flora.—J. M. C.

NOTES FOR STUDENTS

Prothallia and sporelings of lycopods.—Recent investigations have added greatly to our knowledge of some difficult prothallia and sporelings of lycopods and, with researches now well advanced, may make these phases of the life history as clear as in the common ferns. The Lycopodiales and Psilotales will be considered separately.

LYCOPODIALES.—Among the investigators who have studied the prothallia of *Lycopodium*, two have been preeminent both in field and laboratory work, namely, TREUB, who devoted his attention to the tropical species of Java, and BRUCHMANN, who studied species of the northern temperate zone. A third investigator of the first rank must now be added, the Rev. J. E. HOLLOWAY, who has discovered and studied the prothallia and sporelings of various New Zealand species of *Lycopodium*, so that species of the southern temperate zone are now represented. Three papers[3] have already appeared and the investigation is still in progress.

The introductory paper deals with *L. volubile*, *L. scariosum*, *L. densum*, *L. laterale*, *L. cernuum*, and *L. Billardieri*, all of which, except *L. cernuum*, are confined to the islands and countries of the south Pacific. He found prothallia of all except *L. densum*, so that 4 species are recorded for the first time, *L. cernuum* having been described by TREUB. Only a brief mention is made of the prothallia, the paper dealing, as its title indicates, with the comparative anatomy. The structure of the stele in young and adult plants is compared, and it is clearly shown that the radial type is primitive and that the banded type is derived from it.

[3] HOLLOWAY, J. E., A comparative study of the anatomy of six New Zealand species of *Lycopodium*. Trans. New Zealand Inst. **42**:356–370. *pls. 31–34*. 1909.

———, Studies in the New Zealand species of the genus *Lycopodium*. Part I. Trans. New Zealand Inst. **48**:253–303. *pls. 17, 18, figs. 102*. 1916.

———, Studies in the New Zealand species of the genus *Lycopodium*. Part II. Methods of vegetative reproduction. Trans. New Zealand Inst. **49**:80–93. *pls. 8, 9, figs. 24*. 1917.

The second paper deals with 11 species, including the 6 already mentioned, and adding *L. varium*, *L. Drummondii*, *L. fastigiatum*, *L. ramulosum*, and *L. Selago*. Since all these species, with the exception of *L. cernuum* and *L. Selago*, are rather unfamiliar to European and American botanists, the writer describes the habit, habitat, and environmental conditions. The ecological treatment, based upon an immense amount of field work, is particularly interesting, since some of the species are epiphytic and some terrestrial, and, of the latter, some belong to wet and some to dry habitats. Young plants and prothallia are not found in localities where adult plants are abundant, but in places like roadside cuttings where the soil has been disturbed. It is estimated that 15 years may elapse from the germination of the spore of *L. fastigiatum* to the fully developed prothallium; while species like *L. cernuum*, *L. ramulosum*, and *L. laterale* develop their more or less aerial and green prothallia in a single season.

Since the 11 species described by TREUB, BRUCHMANN, and others showed 5 distinct types of prothallia, it is surprising to find that among the various prothallia discovered by HOLLOWAY, no strictly new type has appeared. There are interesting variations, but the divergences are not sufficient to warrant an additional category. He believes that the *Lycopodium* prothallium is in a plastic stage of evolution, and that the various types have not been genetically distinct from a very remote period, but have diverged from the *L. cernuum* type, which now includes *L. inundatum*, *L. salakense*, *L. laterale*, and *L. ramulosum*, and is the only one which has shown a protocorm stage in the embryogeny. In *L. laterale* and *L. ramulosum* a protocorm grows out into a rhizome-like structure, the extension consisting largely of the swollen bases of the successive pairs of protophylls. The stem apex, with the root rather close to it, appears at the end farthest from the foot. Vascular tissue develops between the two apices, so that this region becomes the permanent axis of the plant. An examination of a large number of protocorms in various stages of development brings HOLLOWAY to the conclusion that the organ may be regarded as a physiological specialization to carry the plant over the dry season, and that too much phylogenetic significance should not be attached to it. Such an interpretation would accord, more or less, with BOWER'S "gouty interlude" theory.

The vascular anatomy of the adult plant was studied in 11 species, and in 8 of these the sporeling was also available. In the sporeling there is, at first, a single crescentic group of protoxylem embracing a single group of protophloem; later, the structure becomes diarch, triarch, tetrarch, etc., by the splitting of protoxylem groups, so that the pattern assumes the radial arrangement, the banded condition coming later. In the adult plant, the radial type is found in *L. Selago*, *L. Billardieri*, and *L. varium;* a mixed type in *L. cernuum*, *L. laterale*, and *L. Drummondii;* and a parallel type in *L. volubile*, *L. densum*, *L. fastigiatum*, and *L. scariosum*. The general conclusion is that the various sections of the genus have not been separated from very

ancient times, but that there are rather close interrelationships in which points of contact and divergence may be traced.

The latest paper, issued in July, 1917, deals with methods of vegetative propagation, both gametophytic and sporophytic. In prothallia, vegetative multiplication is accomplished by decay of intermediate parts of elongated specimens and by the isolation of branches in irregular forms. In the sporophyte, methods are more diversified. Bulbils, like those so well known in the *L. Selago* section, are common. In *L. cernuum* bulbils are formed which look exactly like protocorms, except that there is no foot; some of these have as many as 6 protophylls. Reproduction by root tubercles was found in *L. cernuum* and *L. ramulosum*. In the latter species gemmae are produced from cortical cells of the root and even detached leaves may bear bulbils resembling the protocorms of the species. Finally, the elongated protocorms of *L. laterale* and *L. ramulosum* may give rise to new plants by branching and by budding.

Holloway is continuing his studies and, with abundant material and opportunities for observation, will doubtless give us accounts of the internal structures of prothallia and protocorms and especially the development of the vascular system of the sporeling and its transition to the vascular system of the adult plant.

Psilotales.—With the exception of Lang's description of a single specimen, provisionally referred to *Psilotum*, the gametophytes of the Psilotales have been entirely unknown. It was expected of Lawson that when he became established in the University of Sydney he would discover these gametophytes and give us an account, since the Psilotales are the only pteridophytes in regard to whose prothallia we have had no information. Two papers[4] have already appeared and another, dealing with the embryogeny, is in preparation. While *Tmesipteris* is epiphytic, notably on tree ferns, Lawson also found it growing in soil, and it was in such a situation that he found prothallia in greatest abundance. *Psilotum* is more xerophytic, growing in clefts in the rocks, but it also thrives in moist situations, even in the spray of waterfalls, and in these moist places most of the prothallia were found.

In some features the gametophytes of the two genera are very similar. Both are subterranean and tuberous, light brown in color, and uniform in tissue, with no differentiation into vegetative and reproductive regions. An endophytic fungus is found in most of the cells, there being no localized fungal regions. Rhizoids come from all parts of the prothallium. Archegonia and antheridia are borne on the same individual and are not localized, but are scattered over all parts of the plant. The antheridia are spherical and produce a large number of coiled, multiciliate sperms. The archegonium consists of a

[4] Lawson, A. Anstruther, The prothallus of *Tmesipteris tannensis*. Trans. Roy. Soc. Edinburgh **51**:785–794. *pls. 1–3*. 1917.

———, The gametophyte generation of the Psilotaceae. Trans. Roy. Soc. Edinburgh **52**:93–113. *pls. 1–5*. 1917.

venter which lies below the surface of the prothallium and a straight neck which projects as a short tube beyond the surface. The organization of the axial row was not worked out in detail. One figure shows an archegonium with an egg and two free nuclei in the neck canal.

In minor features the two genera differ. In *Tmesipteris* the archegonia are much more numerous than the antheridia, while in *Psilotum* the reverse is true. The archegonia and antheridia of *Tmesipteris* are about twice the size of those of *Psilotum*. The statement that the gametophyte generation of the Psilotaceae bears no structural resemblance to the prothallium of *Lycopodium* or *Equisetum* seems peculiar. We readily agree that there is no suggestion of *Equisetum* characteristics, but both the descriptions and the numerous excellent figures constantly remind one of *Lycopodium*, especially of the *L. Phlegmaria* type. LAWSON closes with the remark that no new facts were revealed which would discount the view, now generally held, that the Psilotaceae are more nearly related to the extinct Sphenophyllales than to any other known group of pteridophytes. This may be true, for the prothallia of the Sphenophyllales are entirely unknown and probably will remain so; but if they should be discovered, we should expect them to be of the *Equisetum* type. As far as the evidence of prothallia goes, we should guess that it indicates relationship with the Lycopodiales. The investigation of the embryogeny will be awaited with interest, since it will have a more definite bearing upon the problem of relationships.—CHARLES J. CHAMBERLAIN.

Photosynthesis.—BROWN and HEISE[5] have made a careful study of the experiments of various investigators on the relation of light intensity to photosynthetic rate. They conclude that "the published work on photosynthesis does not warrant the general conclusion that carbon dioxide assimilation in plants is proportional to the light intensity. Instead they indicate a progressively smaller augmentation of the rate of assimilation for each increase in light intensity. This decrease in rate of augmentation continues until a point is reached at which further increase in light produces no measurable increase in assimilation."

BROWN and HEISE[6] have also scrutinized the literature on the effect of temperature on photosynthetic rate and have come to the following surprising conclusions. The temperature coefficients (Q_{10}) lie between 1 and 1.4. They are smaller than those for most vital phenomena which have values agreeing with the Van't Hoff law. These coefficients are of a magnitude that indicates that photosynthesis is a purely photochemical process.

[5] BROWN, W. H., and HEISE, G. W., The relation between light intensity and carbon dioxide assimilation. Philippine Jour. Sci. **12**:85–95. 1917.

[6] ———, The application of photochemical temperature coefficients to the velocity of carbon dioxide assimilation. Philippine Jour. Sci. **12**:1–24. 1917.

These conclusions are quite out of accord with those of the principal investigators in this field. KANITZ,[7] in his monograph on temperature and life processes, gives the following table, calculated from the experiments of MATTHAEI on the cherry laurel leaf, probably the most nearly error-free piece of work done upon carbon assimilation as effected by temperature.

Temperature	Assimilation CO_2	Q_{10}
−6	0.2	
0	1.75	28.7
10	4.2	2.4
20	8.9	2.12
30	15.9	1.70
37	23.8	1.81
40.5	14.9	0.23

KANITZ points out that the Van't Hoff law applies between 0 and 37° C. He also emphasizes the fact that the coefficient is excessive near the minimum temperature for the process and too small near the maximum, as is true for vital processes generally. The coefficients give no indication that photosynthesis is a purely photochemical process. BAYLISS[8] classifies it as a complex photochemical reaction with increased energy; it results from the combination of purely chemical reactions with photochemical effects. The purely chemical phases seem to be the rate-determining portion, hence the high temperature coefficients. BOVIE[9] gives a similar interpretation of the high temperature coefficients of the process.

The authors misquote KANITZ's formula for calculating Q_{10}. DENNY's review, upon which they depended, misquotes it, due to a typographical error, but they have altered it still further.

NYBERGH attempted to show that photoperception in plants is purely photochemical. His main proof was the small temperature coefficient. DE VRIES has since shown that the coefficient is relatively large and that the process obeys the Van't Hoff law from 10 to 30° C.

It is possible that too much emphasis has been placed upon the size of the temperature coefficient as evidence for the chemical or physical nature of processes in the organism.[10] In the organism, the process often consists of a great number of individual chemical reactions and its rate is the resultant of the rates of all of them. On the other hand, we cannot have too many data on the effect of temperature (or any other factor) on the rate of vital processes or know too much about temperature coefficients which express this effect.—WM. CROCKER.

[7] KANITZ, ARISTIDES, Temperatur und Lebensvorgange. Berlin. 1915.

[8] BAYLISS, W. M., Principles of general physiology (pp. 553–556). London. 1915.

[9] Science N.S. **37**:373–375. 1913.

[10] LEITCH, I., Some experiments on the influence of temperature on the rate of growth in *Pisum sativum*. Ann. Botany **30**:25–46. 1916.

Osmotic concentration and habitat.—The influence of habitat and environmental conditions upon the sap concentration of leaf cells has received considerable attention recently from HARRIS and his co-workers. The cryoscopic method has been used in all determinations of the concentration of tissue fluids, and the studies have now become sufficiently extensive to permit comparisons between the average conditions found in plants of different regions. The mangrove vegetation of Jamaica and Florida[11] has been examined with reference to the influence of salinity of soil water on leaf sap concentration. Three species belonging to three different families were used. The sap concentration is high in all of them, 25–50 atmospheres. *Avicennia nitida* develops the highest concentration of the three, but shows the least variation with environment. *Rhizophora mangle* gave freezing point depressions equivalent to 22–30 atmospheres, and showed distinctly lower leaf sap concentration in fresh water habitats. *Laguncularia racemosa* responded most noticeably, with about 20 atmospheres in fresh water, 25 atmospheres in normal sea water, and 33 atmospheres on sterile mud flats where the sea water is concentrated by evaporation.

A similar study has been made of the Jamaican Blue Mountain rain forest vegetation,[12] where the rainfall averages from 100–130 inches per year. Only terrestrial plants have been reported upon so far, coming from four distinct sub-habitats: the ruinate of leeward slopes, leeward ravines, ridges, and windward slopes and ravines. The plants of each habitat are grouped as ligneous and herbaceous. Distinct differences in the concentration of the tissue fluids of plants growing in each habitat were found, and, as in previous work, the ligneous plants of each type habitat proved to have more concentrated leaf sap than the herbaceous group. The average osmotic concentration of the ligneous plants is about 11.44 atmospheres, and of herbaceous plants 8.8 atmospheres. These figures are lower than for any region thus far investigated, and contrast strongly with values obtained from our southwestern deserts, where herbaceous plants reach 15 atmospheres and ligneous plants 25. In ascending order of sap concentration, the four sub-habitats stand as follows: the windward slopes and ravines, leeward ravines, ridge forests, and ruinate.

Variation in leaf sap concentration with height of insertion on the tree[13] has been studied also, and DIXON'S results confirmed, that the concentration of sap is almost always higher, the higher up the leaf is on the tree. Since, however, the specific electrical conductivity of the sap usually decreases from lower to higher levels, it is probable that photosynthetic sugars are produced

[11] HARRIS, J. ARTHUR, and LAWRENCE, JOHN V., The osmotic concentration of the sap of the leaves of mangrove trees. Biol. Bull. **32**:202–211. 1917.

[12] ———, The osmotic concentration of the tissue fluids of Jamaican montane rain forest vegetation. Amer. Jour. Bot. **4**:268–298. 1917.

[13] HARRIS, J. ARTHUR, GORTNER, ROSS AIKEN, and LAWRENCE, JOHN V., The relationship between the osmotic concentration of leaf sap and height of leaf insertion in trees. Bull. Torr. Bot. Club **44**:267–286. 1917.

more abundantly in the upper parts of the trees, and are the cause of increased sap concentration. Any agreement between observed increments of osmotic pressure and theoretical values calculated from the increased hydrostatic head and resistance to be overcome in the tracheae by virtue of higher position is regarded as a coincidence, and not as a proof of adjustment on the part of the cells to the back pull of increased head and resistance.—CHARLES A. SHULL.

Antagonism.—Antagonism between iron and manganese in their effects on the growth of two varieties of wheat has been investigated by TOTTINGHAM and BECK.[14] Manganous chloride in water cultures even in low concentrations reduces root growth, but when ferric chloride is added in about equimolecular (0.00001 M) concentration the deleterious effects of the manganous salt are overcome. The two varieties of wheat used did not give exactly the same results, and it is believed that effects will depend on variety to a certain extent. Thus the amount of reserve iron in the seed would influence the response of the plant to variations in supply of salts of these two metals. In very dilute solutions the manganous chloride seemed to have stronger effects than ferric chloride on the color and growth, while in higher concentrations (0.001 M) the iron salt had more effect than the manganese. Although the concentrations used approach that of these salts in the soil solution, no conclusions as to antagonism in soil cultures can be drawn because of the great variety of other salts and conditions which might modify the result.

SKINNER[15] has studied the effects of manganese sulphate and some other inorganic substances in overcoming the unfavorable action of vanillin and salicylic aldehyde on plants grown in culture solutions of varying composition. He finds that vanillin reduces the growth of cow peas, but the presence of nitrate reduces the unfavorable action, and may even entirely overcome the reduction of growth caused by vanillin. The harmful effects of salicylic aldehyde in 5 and 10 ppm. concentrations on wheat seedlings were entirely overcome by manganese sulphate in 10 ppm. concentration; and the harmfulness of vanillin was also partially overcome by manganese sulphate. He explains the action of nitrate and manganese on the ground that they favor root oxidation, whereby the harmful organic compounds are oxidized and are not permitted to influence growth unfavorably.—CHARLES A. SHULL.

The embryo sac of Aster and Solidago.—These much investigated embryo sacs have been studied again, this time by PALM,[16] a pupil of ROSENBERG.

[14] TOTTINGHAM, W. E., and BECK, A. J., Antagonism between manganese and iron in the growth of wheat. Plant World **19**:359–370. 1916.

[15] SKINNER, J. J., The effect of vanillin and salicylic aldehyde in culture solution and the action of chemicals in altering their influence. Plant World **19**:371–378. 1916.

[16] PALM, BJ., Zur Embryologie der Gattungen *Aster* und *Solidago*. Acta Horti Bergiani **5**:1–18, *figs.* 27. 1914.

Aster novae-angliae and *Solidago serotina* were the principle species under examination. Several figures show that a tetrad of four megaspores is formed, as would have been expected. In regard to later stages, PALM disagrees with the results of the reviewer[17] and the subsequent study of Miss OPPERMAN,[18] for he claims that the extensive development in the antipodal region is due to the growth of the lower megaspores of the tetrad. His series is far from complete, however, and his figures, interpreted in this way, do not show any antipodal cells. While my own series, published more than 20 years ago, was incomplete, and Miss OPPERMAN'S lacked stages in the early development, I see no reason why either of us should change our view that the chalazal development results from the enlargement of one or more of the antipodal cells. To prove his claim, PALM should present figures of the 8-nucleate stage of the sac, followed by a close series showing the disappearance of the antipodal cells or nuclei. Since such figures are lacking, we prefer to interpret the enlarged cells in the chalazal region as antipodals and not as persistent megaspores.—CHARLES J. CHAMBERLAIN.

The vegetation of Connecticut.—Continuing the studies previously noted,[19] NICHOLS[20] in a fourth paper has considered the vegetation of the swamps and bogs of Connecticut. The latter presents the more interesting group of plant associations, conspicuous among which is the bog forest of *Picea mariana* and *P. rubra*, occasionally supplemented by *Pyrus americana*, constituting a remarkable aggregation of northern trees. These trees, together with shrubs and herbs of northern affinities, lead the author to a consideration of the much discussed question of the origin of bog vegetation, resulting in the opinion that the vegetation is that of a relic swamp type, representing the vestigial remnants of a more northern type of flora which dominated the region within a geological time decidedly more recent than the Pleistocene.

In a similar connection it is interesting to note that in the fifth paper attention is directed to the fact that the rock ravine is second only to the bog for its display of northern species. This paper gives a careful survey of the plant communities associated with stream erosion and deposition. None of the associations are of striking interest, but it serves to round out a comprehensive study of the vegetation of the state.—GEO. D. FULLER.

[17] CHAMBERLAIN, C. J., The embryo sac of *Aster novae-angliae*. BOT. GAZ. **20**: 205–212. *pls. 15, 16*. 1895.

[18] OPPERMAN, MARIE, A contribution to the life history of *Aster*. BOT. GAZ. **37**:353–362. *pls. 14, 15*. 1914.

[19] BOT. GAZ. **59**:159–160. 1915.

[20] NICHOLS, G. E., The vegetation of Connecticut. IV. Plant societies of the lowlands. V. Plant societies along rivers and streams. Bull. Torr. Bot. Club **42**:169–217. *figs. 15*. 1915; **43**:235–264. *figs. 11*. 1916.

GENERAL INDEX

Classified entries will be found under Contributors and Reviewers. New names and names of new genera, species, and varieties are printed in **bold face** type; synonyms in *italics*.

A

Abronia exaltata 337
Acamptopappus Shockleyi 343
Acremonium **meliola** 234
Adams, J. F., work of 373
Addisonia 195, 491
Aecial stage of Puccinia oxalidis 475
Aecidium Enceliae 472
Africa, new fungi from 482
Age and area hypothesis 486
Algae, of Devils Lake 491; of Hawaiian archipelago, 42, 121
Allard, H. A. 175
Allionia linearis 337
Allium **scissum** 58
Alway, F. J., work of 196
Amaranthus deflexus 336
Ammonia and ammonium salts in plants 117
Amobroma sonorae 340
Anamomis 483
Anatomy of Betulaceae 198; of Solidago 250
Andes, Uredinales of the 460
Aneura 285
Angiosperms, evolution of vessels in 83
Antagonism 571
Anthoceros 285
Antirrhinum Kingii 341
Apogamy in Cyatheaceae 97
Appleman, C. O. 200
Argemone intermedia corymbosa 337
Armstrong, S. F., "British grasses" 365
Arthrobotryum 235; caudatum 238; **dieffenbachiae** 237; **glabroides** 237; **penicillium** 238
Arthur, J. C. 460; work of 373, 481
Ascomycetes 482
Aspidopterys 375
Aster, embryo sac of 571
Astragalus trifiorus 338
Athyrium 375
Atkinson, G. F. 103
Atriplex confertifolia 336

B

Bartholomew, E. T., work of 374
Bartlett, H. H. 560
Basigyne 483
Bayliss, W. M., work of 569
Beauverie, J., work of 373
Beck, A. J., work of 571
Belandra 375
Belonidium leucorrhodinum 228
Berberis Fremontii 337
Bermuda, flora of 564
Betulaceae, anatomy of 198
Bews, J. W., work of 286
Biology of rusts 366
Blackman, V. H., work of 281
Blake, S. F., work of 284, 375, 481
Blomquist, H. L., 488
Blomqvist, S. G., work of 489
Blueberry, structure of wood 556
Boerker, R. H., work of 287
Boncquet, Mary, work of 199
Boncquet, P. A., work of 199
Borneo, flora of 482
Botrychium virginianum 375
Boulder Park, Colorado, successions of vegetation in 493
Braun, E. Lucy 191; work of 492
Brierly, W. B., work of 288
Briggs, L. J., work of 197, 281
Britton, N. L., "Flora of Bermuda" 564; work of 284
Brodiaea **coronaria** 58
Brooks, C., work of 115
Brown, J. G. 193
Brown, Mabel M., work of 376
Brown, W. H., work of 568
Bryophyllum calycinum, experiments with 150; regeneration of 191
Bud sport on Syringa persica 560
Burt, E. A., work of 284, 482
Butters, F. K., work of 375
Byrsonima 284

C

Calandrinia ambigua 337
Californian plants 120, 334
Calonectria erubescens 232; **graminicola** 232; melioloides 231
Canada, plant formations of 120
Carbon, assimilation of organic 543; nutrition 120
Cassia armata 338
Catacorolla in Nicotiana 178
Cephaelis 285
Ceratodon, assimilation of organic carbon by 543
Chamberlain, C. J. 480, 491, 565, 571
Chase, Agnes, work of 285
Cheilanthes Feei 334
Child, C. M. 274
Chilton, C., work of 118
Chrysler, M. A. 363
Chrysocelis Lupini 463
Cladium Mariscus californicum 335
Clarkia 59; **amoena** 62; **arcuata** 62; **Arnottii** 64; **biloba** 60; **caurina** 62; **decumbens** 64; **delicata** 60; **epilobioides** 60; **gracilis** 63; pulchella 62; **purpurea** 64; **quadrivulnera** 63; rhomboidea 63; **Romanzovii** 63; **superba** 60; **viminea** 64
Cleistogamy in Heteranthera 197
Clements, F. E., work of 484
Cleptomyces Lagerheimianus 464
Clibadium 375
Clithris clusiae 554; **minor** 554; **pandani** 555; systematic relationship of 552
Clitocybe acromelalga 110
Cobb, Frieda 560
Cockayne, A. H., work of 119
Cockayne, L., work of 118
Coleosporium Senecionis 462
Collins, G. N., work of 118
Colorado, vegetation of 196
Columella in Marchantia 91
Condalia lycioides 330
Coniophora 284
Coniothyrium **glabroides** 234
Connecticut, vegetation of 572
Contributors: Allard, H. A. 175; Appleman, C. O. 200; Arthur, J. C. 460; Atkinson, G. F. 103; Bartlett, H. H. 560; Blomquist, H. L. 488; Braun, E. Lucy 191; Brown, J. G. 193; Chamberlain, C. J. 480, 491, 565, 571; Child, C. M. 274; Chrysler, M. A. 363; Cobb, Frieda 560; Cook, M. T. 194, 195; Coulter, J. M. 194, 195, 196, 197, 198, 284, 375, 481, 491, 492, 564; Coulter, M. C. 116, 486; Cowles, H. C. 564; Cribbs, J. E. 91; Crocker, W. 117, 199, 287, 370, 485, 487, 490, 568; De Vries, H. 377; East, E. M. 118; Elmore, C. J. 186; Fitzpatrick, H. M. 201; Flint, Esther M. 556; Fuller, G. D. 119, 120, 195, 196, 197, 281, 283, 285, 286, 288, 479, 481, 483, 487, 488, 492, 572; Gericke, W. F. 344; Harsch, R. M. 475; Hasselbring, H. 366; Hitchcock, A. S. 365; Ichimura, T. 199; Jackson, H. S. 289; Jones, D. F. 324; Jørgensen, I. 520; Langdon, LaDema M. 313; Loeb, J. 150; Long, E. R. 354; Long, W. H. 475; Macbride, J. F. 58; MacCaughey, V. 42, 121; McNair, J. B. 268; Nelson, A. 58; Parish, S. B. 334; Ramaley, F. 196; Rigg, G. B. 197, 359; Robbins, W. J. 543; Robbins, W. W. 493; Rock, J. F. 261; Rose, D. H. 112; Sargent, C. S. 423; Schneider, C. 1; Shull, C. A. 119, 120, 570, 571; Spessard, E. A. 362; Steil, W. N. 562; Stevens, F. L. 227; Stiles, W. 520; Stokey, Alma G. 97; Tehon, L. R. 552; Thompson, W. P. 83, 119; Trelease, W. 480, 490; True, R. H. 71; Wells, B. W. 535; Whitaker, Edith S. 250
Cook, M. T. 194
Cooley, J. S., work of 115
Cooper, W. S., work of 492
Copper sulphate, effect of 490
Correlation, chemical basis of 150
Coulter, J. M. 194, 195, 196, 197, 198, 284, 375, 481, 491, 492, 564
Coulter, M. C. 116, 486
Cowles, H. C. 564
Cribbs, J. E. 91; work of 288
Crocker, W. 117, 199, 287, 370, 485, 487, 490, 568
Cucurbita californica 342
Cyatheaceae, apogamy in 97

D

Davie, R. C., work of 284
Davis, A. R., work of 112, 119
Dearness, J., work of 482
Desiccation of Echinocactus 354
Devils Lake, diatoms of 186
De Vries, H. 377
Diatoms of Devils Lake 186
Dietel, P., work of 372
Dimerium piceum 229
Dimerostemma 375
Double fertilization and heterosis 324
Duggar, B. M., work of 112, 113
Dutch Guinea, vegetation of 488
Dysodia Thurberi 343

E

East, E. M. 118
Echinocactus, desiccation and respiration 354
Elmore, C. J. 186
Elymus cinereus 335
Embryo sac and embryo of Phaseolus 376; of Aster and Solidago 571
Endemism 116
Equisetum, endodermis and prothallium of 491
Evans, A. W., work of 482
Evaporation and soil moisture 483
Evergreens, leaf duration in 197

F

Fawcett, W., work of 284
Ferguson, A., work of 281
Fernald, M. L., work of 284, 375, 482
Fern, method for staining antherozoid 502
Fibers of tension 487
Fischer, E., work of 372
Fitzpatrick, H. M. 201
Flint, Esther M. 556
Flora of Bermuda 564
Freiberg, G. W., work of 113
Frommea 481
Fromme, F. D., work of 372
Fruit drop 370
Fuller, G. D. 119, 120, 195, 196, 197, 281, 283, 285, 286, 288, 479, 481, 483, 487, 488, 492, 572
Fungi, physiology of 112
Fusarium **meliolicolum** 245

G

Ganong, W. F., "Textbook of botany" 104
Gassner, G., work of 366, 371
Gates, F. C., work of 195, 484
Gaultheria 284
Gaura coccinea 340
Gentiana **Covillei** 65
Gericke, W. F. 344
Germination 485; of spores 288; of tree seeds 287
Gibbsia 482
Gibbs, Lilian S., work of 482, 488
Gilia ochroleuca 340
Gillman, J. C., work of 114
Gnetales, evolution of vessels in 83
Gnetum moluccense, anatomy of 110
Gortner, R. A., work of 285, 570
Grallomyces **portoricensis** 245
Grasses of West Indies 285
Grasslands and forests of Washington 283
Grebelsky, F., work of 371

H

Habitat, osmotic concentration and 570
Hanson, H. C., work of 487
Haplopappus eximius 70
Harris, J. A., work of 285, 286, 570
Harsch, R. M. 475
Harshberger, J. W., "New Jersey pine barrens" 479
Hasselbring, H. 366
Hawaiian Archipelago, algae of 42, 121; ornamental trees of 481
Hawkins, L. A., work of 115, 120
Hecke, L., work of 370
Heise, G. W., work of 508
Helminthosporium 230; **glabroides** 240; **guareicolum** 241; **helleri** 242; **melastomacearum** 242; **ocoteae** 241; **panici** 242; **parathesicolum** 242; **philodendri** 242
Hemsley, W. B., work of 284
Herbarium Amboinense 490
Heteranthera, cleistogamy in 197
Heterosis and double fertilization 324
Hill, A. W., work of 284
Hitchcock, A. S., work of 285, 305
Hoar, C. S., work of 198
Hodgson, R. W., work of 376
Holloway, J. E., work of 505
Hooker, D. H., work of 287
Huckleberry, structure of wood 556
Hungerford, C. W., work of 370
Hutchinson, J., work of 375
Hybrids, of maize 118; of Verbascum 488
Hypochaeris glabra erostris 343

I

Ichimura, T. 100
Idenburgia 482
Ipomea hirsutula 342
Isoetes melanopoda pallida 334
Isthmospora 244; glabra 244; **spinosa** 244

J

Jaccard, P., work of 487
Jackson, H. S. 280
Jeffrey, E. C., "Anatomy of woody plants" 363
Jones, D. F. 324
Jorgensen, I. 526
Jungelson, A., work of 490

K

Kanitz, A., work of 569
Kashyap, S. R., work of 491
Knight, R. C., work of 281, 282
Kunkel, L. O., work of 373

L

Langdon, LaDema M. 313
La Rivière, Henriette C. C., work of 119
Law of the minimum 287
Lawrence, J. V., work of 285, 570
Lawson, A. A., work of 567
Leaf, duration in evergreens 197; ecological anatomy of 487
Leitch, I., work of 569
Lejeunea 482
Lesage, P., work of 485
Lesquerella Gordoni 337; Palmeri 337
Livingston, B. E., work of 281
Loeb, J. 150; "The organism as a whole" 274
Lonchocarpus 376
Long, E. R. 354
Long, W. H. 475; work of 372
Lupinus 376, 483; flaveculatus 338; pallidus 338
Lycopodiales, prothallia and sporelings of 565
Lycopodium, prothallia of 362
Lycopsis arvensis 341

M

Macbride, J. F. 58
MacCaughey, V. 42, 121
McDougall, W. B., work of 489
McNair, J. B. 268
Macoun, J. M., work of 120
Mains, E. B., work of 114, 369, 370
Maire, R., work of 482
Maize, hybrids of 118
Malte, M. O., work of 120
Mangham, S., work of 199
Marchantia, columella in 91
Marine algae, osmotic experiments with 71
Martin, W. H., work of 282
Mass mutations and twin hybrids of Oenothera grandiflora 377
Meliola, parasites on 227
Menodora spinescens 340
Mentzelia nitens 339; reflexa 339
Mercer, W. H., work of 370
Merrill, E. D., work of 482, 490
Merulius 482
Metrosideros 482
Mistletoe, parasitic on mistletoe 193
Mohavea breviflora 341
Moore, G. T., work of 491
Muhlenbergia repens 335
Mushroom, a new poisonous 109; edible and poisonous 489
Myxomycetes 483

N

Naemosphaera **hyptidicola** 233
Natal vegetation 286
Nectria **meliolicola** 231; **portoricensis** 231
Nelson, A. 58
Nemophila heterophylla **tenera** 66; parviflora Austinae 67; pedunculata **densa** 66; pedunculata **sepulta** 65
New Guinea, new species from 482
New Zealand Biological Station 118
Nichols, G. E., work of 572
Nicotiana, abnormalities in 175; catacorolla in 178; synanthic blossoms in 175
Nitrogen determinations 119
North American flora 492

O

Oenothera, grandiflora, mass mutations and twin hybrids 377; multijuga 340; primiveris 340
Ohio, vegetation of 492
Opperman, Marie, work of 572
Opuntia acanthocarpa 330; mojavensis 339; Parryi 340
Oreocarya echinoides 341
Osmotic concentration and habitat 570; experiments with marine algae 71
Osterhout, G. E., work of 375
Oxystylis lutea 337

P

Palicourea 285
Palm, B., work of 571
Pamburus 376
Paranectria **meliolicola** 232; **miconiae** 233
Parish, S. B. 334; work of 120
Paspalum Larranagae 334
Pease, Vinnie A., work of 197
Peck, Charles Horton, sketch of 103
Pelea 261; auriculaefolia 266; cinerea Hawaiiensis 265; cinerea **rubra** 264; cinerea sulfurea 265; **Gayana** 262; Knudsenii 266; **recurvata** 267; sapotaefolia 261; Wawraeana 265
Pennisetum villosum 335

Pennsylvania, vegetation of 288
Pentstemon **Albrightii** 69; **pandus** 69; perpulcher 67; subulatus 341
Perisporium meliolae 228; **paulliniae** 228
Permeability, quantitative measurement of 526
Phacelia calthifolia 341
Phaseolus, embryo sac and embryo 376
Photosynthesis 568
Phyllogonum luteolum 336
Physalis hederaefolia 341
Physical system, a living 197
Physiological diseases 199
Picea excelsa, variation in 491
Pickering, S., work of 492
Piemeisel, F. J., work of 374
Pilularia americana 334
Pittier, H., work of 376
Plant, communities and sap concentration 285; physical factors in distribution 198
Platydesma 261, 266
Pleiospermium 376
Pleurostachys 284
Polygonum 481
Porto Rico, Meliolicolous parasites 227
Prenanthes **hastata** 70
Prothallia 565; of Lycopodium 362; of Psilotales 567
Pseudonectria **pipericola** 230
Psilostrophe Cooperi 343
Psilotales, prothallia of 567
Psychotria 285
Puccinia **Acnisti** 470; **Arthuriana** 295; **Bambusarum** 467; Becki 293; carduaceous species of 280; **cuzcoensis** 471; **discreta** 308; egregia 306; elephantopodis 311; **erratica** 294; **fraterna** 297; fuscella 299; **hyalina** 298; Hydrocotyles 470; **idonea** 304; **inaequata** 309; **insulana** 296; **Kuntzii** 310; Leptoderma 312; Le Testui 298; Lorentzii 301; malvacearum 470; membranacea 294; Mogiphanis 469; **Nicotianae** 470; **notha** 305; oxalidis, aecial stage of 475; paupercula 311; pinguis 310; Piptocarphae 311; **praealta** 306; **rata** 303; Roseanae 468; rotundata 307; semiinsculpta 301; simplex 335; Spegazzinii 471; Spilanthis 472; unicolor 472; Vernoniae 299, 312; Vernoniae-mollis 296; vernoniicola 296; vernoniphila 298

Q

Quercus alba 434; alba **latiloba** 435; ray system of alba 313; **Andrewsii** 455; annulata 443; austrina 435; **beaumontiana** 451; **Bushii** 453; cinerea 433; coccinea **tuberculata** 420; **Cocksii** 459; **Comptonae** 456; dubia 452; **guadalupensis** 454; **Harbisonii** 458; **Hastingsii** 450; **jolonensis** 456; laurifolia 432; laurifolia tridentata 433; **Lowellii** 459; Mellichampii 451; Mohriana 443; Muehlenbergii **Brayi** 442; nigra 428; nigra **tridentifera** 420; **oviedoensis** 459; **rhombica** 430; **rhombica obovatifolia** 431; rubra 426; rubra leucophylla 428; rubra pagodaefolia 427; rubra triloba 427; Shumardii 424; Shumardii **Schneckii** 425; stellata 436; stellata **anomala** 428; stellata araniosa 441; stellata **attenuata** 437; stellata **Boyntonii** 437; stellata Margaretta 440; stellata **Palmeri** 439; stellata **paludosa** 441; stellata **parviloba** 438; stellata **rufescens** 430; subfalcata **microcarpa** 454; texana 423, 426; texana **chesosensis** 423; texana **stellipila** 424; utahensis **submollis** 442; virginiana 443; virginiana **dentata** 448; virginiana **eximia** 447; virginiana **fusiformis** 448; virginiana **geminata** 445; virginiana **macrophylla** 447; virginiana maritima 449; virginiana **pygmaea** 440; virginiana **virescens** 446

R

Ramaley, F. 196
Raritebe 483
Ray system of Quercus alba 313
Redwood distribution 492
Reed, H. S., work of 113
Regeneration of Bryophyllum 191
Rendle, A. B., work of 284
Respiration of Echinocactus 354
Reviews: Armstrong's "British grasses" 365; Britton's "Flora of Bermuda" 564; Ganong's "Textbook of botany" 194; Harshberger's "New Jersey pine barrens" 470; Jeffrey's "Anatomy of woody plants" 363; Loeb's "Organism as a whole" 274; Robbins' "Botany of crop plants" 195, 564; Rock's "Ornamental trees of Hawaii" 481; Taubenhaus' "Culture and diseases of the sweet pea" 194; Trelease's "Plant materials of decorative gardening" 194; West's "Algae" 480
Reynolds, E. S., work of 373
Rhizina undulata, sexuality in 201
Rhus diversiloba, secretory canals of 208
Rhynchospora 284
Rhysolepis 375
Rigg, G. B. 197, 359
Riseleya 284

Robbins, W. J., 543
Robbins, W. W. 493; "Botany of crop plants" 195, 564; work of 196
Rock, J. F. 261; "Ornamental trees of Hawaii" 481; work of 482
Rocky Mountains, subalpine plants of 195
Rose, D. H. 112; work of 113
Rubiaceae 483
Russell, E. J., work of 115
Rusts, biology of 366
Ruta chalapensis 339
Rydberg, P. A., work of 195

S

Sagina apetala 337
Salicornia utahensis 336
Salix amygdaloides **Wrightii** 14; Bonplandiana 17; Bonplandiana pallida 19; Bonplandiana **Toumeyi** 20; cana 38; conspectus of 1; exigua 25; exigua **stenophylla** 25; Gooddingii 12; Hartwegii 28; Humboldtiana 6; Humboldtiana **Martiana** 8; Humboldtiana **stipulacea** 7; jaliscana 16; laevigata 21; lasiolepis 31; longifolia angustissima 26; longipes 21; longipes **venulosa** 14; mexicana 29; nigra **Lindheimerii** 9; **oxylepis** 34; paradoxa 35; paradoxa ajuscana 37; Peasei 482; **Rowleei** 31; Rowleei **cana** 34; **Schaffnerii** 30; sessilifolia **leucodendroides** 26; taxifolia 23; taxifolia **microphylla** 24; funerea 341
Sap concentration and plant communities 285
Sargent, C. S. 423
Saugetia 285
Scirpus robustus paludosus 335
Schmitz, H., work of 113
Schneider, C. 1
Secretory canals of Rhus diversiloba 268
Sequoia sempervirens, distribution of 492
Severy, J. W., work of 113
Sexuality in Rhizina undulata 201
Shantz, H. L., work of 281
Shive, J. W., work of 282
Shreve, F., work of 198
Shull, C. A. 119, 120, 570, 571
Sinnott, E. W., work of 116
Sisyrinchium **boreale** 58; idahoense **birameum** 58
Skinner, J. J., work of 571
Small, J. K., work of 376, 483
Smith, C. P., work of 376, 483
Smith, E. F., work of 114, 196
Smith, J. J., work of 483
Soil moisture 196; and evaporation 483; toxins 492
Solanum effects of rest and no-rest periods 344
Solidago, anatomy of 250; embryo sac of 571
Speight, R., work of 118
Sperms of ferns, method for staining 562
Spessard, E. A. 362
Sphagnum, growth of trees in 359
Sphenospora **Berberidis** 405
Sporobolus flexuosus 335
Stakman, E. C., work of 374
Stanleya elata 338
Steil, W. N. 562
Stephani, F., work of 285
Stevens, F. L. 227
Stiles, W. 520
St. John, H., work of 375
Stokey, Alma G. 97
Strychnos 284
Sturgis, W. C., work of 483
Successions of vegetation in Boulder Park, Colorado 403
Sugar, translocation of 199
Swingle, W. T., work of 376
Synanthic blossoms in Nicotiana 175
Syringa persica, bud sport on 560

T

Taal volcano, revegetation of 195
Taubenhaus, J. J., "Culture and disease of the sweet pea" 194
Tehon, L. R. 552
Tetracoccus Hallii 339
Thiel, A. F., work of 484
Thomas, N., work of 281
Thompson, W. P. 83, 119
Tonestus **eximius** 70
Tottingham, W. E., work of 571
Transpiration studies 281
Treboux, O., work of 369
Trelease, W. 480, 490; "Plant materials of decorative gardening" 194
Trifolium gracilentum reductum 338; Leibergii 58
True, R. H. 71
Turrill, W. B., work of 284
Twin hybrids and mass mutations of Oenothera grandiflora 377

U

Uredinales of the Andes 460
Uredo Erythroxylonis 473
Uromyces Cestri 467; crassipes 466; elatus 466; Howei 467; leptodermus 466
Uropyxis quitensis 464

V

Vaccinium, structure of wood 556
Verbascum hybrids 488

W

Washington, grasslands and forests of 283
Weaver, J. E., work of 282, 283, 483, 484
Weevers, Th., work of 117
Wells, B. W. 535
Wernham, H. F., work of 285, 483
West Indies, grasses of 285
West, . S., "Algae" 480
Western plant studies 58
Wheat, new disease of 196
Whitaker, Edith S. 250
Willis, J. C., work of 116, 486
Wittrock, V. B., work of 491
Wylie, R. B., work of 197

Y

Yucca baccata 336

Z

Zeller, S. M., work of 112
Zoocecidia of N.E. United States and eastern Canada 535